

# INSECTES SOCIAUX

BULLETIN DE L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX



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# SOME METEOROLOGICAL FACTORS AFFECTING THE FORAGING OF *FORMICA SUBNITENS* CREIGHTON (HYMENOPTERA: « FORMICIDAE ») (1)

by

Gordon L. AYRE

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During 1954 and 1955 the feeding habits of the ant *Formica subnitens* Creighton were investigated at Westbank, British Columbia. The number of ants active and the periods when they were active influenced both the numbers and species of insects taken as food. This paper presents the data obtained from initial field studies of some meteorological factors affecting the foraging activities of *F. subnitens*.

## *Materials and methods.*

These studies were conducted in a 10-acre field five miles north of Westbank during the summer of 1955. The field contained 89 colonies of *F. subnitens* uniformly distributed. The diameter and height of each nest were measured and a nest of average size was chosen for study. The detritus dome of the nest chosen was 20 inches in diameter and six inches in height. The nest was covered with a one-inch mesh wire screen over a square wood frame to protect it from predation by flickers (*Colaptes* spp.), which were common in the area and which frequently dug out the nests in search of ant larvae and pupae. Four main trails, two of which branched repeatedly, radiated from the nest. The foraging area of the colony (fig. 1) was approximately 2,500 square feet and contained all the predominant plants found in the region. These included a pine tree, *Pinus ponderosa* Laws., Kentucky blue grass, *Poa pratensis* L.; several species of bunch grass; Klamath weed, *Hypericum perforatum* L.; and wild rose, *Rosa* sp.

Census points were established three feet from the nest on each trail and the numbers of ants passing these points were recorded.

BEGINNING AND END OF FORAGING. — An attempt was made to determine the meteorological conditions at the times when trail activities started and stopped. Records were made at one to 10 intervals throughout the study periods, depending on rate of change in conditions. While the ants were active the numbers of ants travelling to and from the nest on one trail were recorded at one-minute intervals for a minimum of 30 minutes. A minimum of three sets of data were collected for each of four study periods, i.e., morning start, morning stop, afternoon start, and evening stop.

AREA AND TYPES OF FORAGING. — An attempt was made to determine the numbers of ants on different trails and the type of foraging in which each ant was engaged. Only the numbers returning to the nest were recorded and these were classified as

(1) Contribution No. 3576, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

to whether they were carrying insect food, thatch, or aphid secretions, or were returning "empty handed". Distension of the gaster was considered to indicate that an ant carried aphid secretions. These observations were made on each trail for three five-minute intervals. Counts were made for one complete day once every two weeks and were repeated every four hours from 4.00 a.m. until activity ceased.

**FLUCTUATION IN FORAGING.** — At intervals of two weeks from May to August the number of ants travelling to and from the nest on one trail during three consecutive five-minute periods was recorded once each hour during the entire period of ant activity during one day. Meteorological data were taken at the beginning of each five-minute period.

Standard air temperature, air temperature at 1/4 inch above the ground, soil surface temperature, brood chamber temperature, relative humidity, light intensity, atmospheric pressure, and cloud cover were recorded for all studies of ant activity. Standard air temperature and relative humidity were recorded on a hygrothermograph placed in a standard weather screen approximately 30 feet east of the nest. Soil surface temperature, air temperature at 1/4 inch above the ground, and brood chamber temperature were read from a portable potentiometer calibrated in degrees Fahrenheit. A selector switch was used in conjunction with the potentiometer to allow permanent connections for all thermocouple leads. Single junction thermocouples of No. 24 plastic-covered iron-constantan wire were used for temperature of the soil surface and the air at 1/4 inch above the ground. The soil surface thermocouple was an open loop 2 1/2 inches in diameter placed directly on the soil surface. The leads to this thermocouple were placed so that they were never shaded from solar radiation. The thermocouple 1/4 inch above the soil was a closed loop with the contacts bent parallel to the soil surface. A small aluminium shield, which allowed maximum air circulation but prevented direct solar radiation from reaching the thermocouple, was used. The lead to this thermocouple was shaded for three feet behind the junction.

Brood chamber temperatures were taken with a commercially prepared, chrome-plated 24-inch iron pencil thermocouple. This was inserted at an angle into the brood chamber from the side of the nest. The exposed portion of the thermocouple was protected from solar radiation by a shield of aluminium foil.

Light intensities were measured by reading reflected light intensity on a light meter mounted at a 15° angle above a swivel-top table. Brown wrapping paper was used as a reflective surface on the table and was replaced daily to prevent changes in reflective properties caused by weathering. The table and meter were tilted to obtain maximum readings.

Atmospheric pressures were recorded on a microbarograph approximately one mile north of the study area.

Cloud cover was estimated in tenths of the sky covered by cloud.

Notes were kept on other phenomena such as precipitation, thunderstorms, dew formation, and sunrise and sunset whenever activity studies were being made.

## RESULTS AND DISCUSSION

### *Beginning and end of foraging.*

Table I shows the range of meteorological conditions within which *F. subnitens* was active on the foraging trails. On cool days, i.e., during spring and fall and on overcast days during the summer months, there was one period of trail activity daily. On warm days, i.e., clear and partially clouded days during the summer, there were two periods, one occurring in the late morning and the other in the afternoon.



TABLE I. — AVERAGE METEOROLOGICAL CONDITIONS, AND RANGES (IN PARENTHESES), AT THE TIME OF THE START AND STOP OF FORAGING OF *F. subnitens*.

PERIOD	TEMPERATURE (°F.)					RELATIVE HUMIDITY (%)	ATMOSPHERIC PRESSURE (INCHES OF MERCURY)	LIGHT (FOOD CANDLES OF REFLECTED LIGHT)
	1/4 inch above soil	Soil surface	Average	Brood Chamber	Standard air			
Morning start	50.8 (50.0-51.5)	50.6 (50.5-50.7)	50.7 (50.2-51.0)	69.4 (66.2-74.0)	49.7 (48.0-52.0)	88.5 (81.0-97.5)	30.03 (29.90-30.16)	384 (67-600)
Morning stop	94.7 (90.0-98.5)	134.0 (127.0-145.7)	114.4 (108.5-121.4)	83.3 (78.0-84.5)	72.2 (66.2-77.0)	44.8 (32.0-52.5)	29.99 (29.86-30.14)	4,417 (1,200-1,500)
Afternoon start	100.9 (85.0-110.0)	128.0 (123.0-137.0)	113.2 (104.5-120.7)	92.6 (81.0-100.5)	80.5 (76.0-88.0)	28.2 (25.0-32.0)	29.93 (29.86-30.04)	1,100 (800-1,400)
Evening stop	46.5 (45.5-48.0)	52.2 (51.0-53.0)	49.3 (48.2-50.5)	72.7 (71.0-75.0)	56.2 (54.5-58.0)	73.2 (70.0-79.5)	30.09 (29.98-30.18)	0 (0)

TEMPERATURE.—The great variation in standard air temperatures indicates that this factor was not significant in the beginning and ending of trail activity. The measure was unsatisfactory for determining the temperatures experienced by the ants because of varying vertical temperature gradients.

The temperatures in the brood chamber, at 1/4 inch above the ground, and at the soil surface appeared to have a direct influence on ant activity.

However, brood chamber temperature did not seem to influence trail activity directly, as it showed a great variation at the start and stop of trail activity. Nests of *F. subnitens* may go to a depth of five feet and hence there is a range in temperature within the nest. The brood chamber temperatures represent only one section of the nest. Moreover, the temperatures within the nest never reached the extremes of external temperatures. During these investigations the high temperatures apparently required for limiting trail activity never occurred within the nest. Consequently, though brood chamber temperature has an influence on the ants, it is not considered important in initiating or limiting trail activity.

The temperatures at 1/4 inch above the ground and on the ground surface influenced trail activity directly. The relatively narrow range of these two temperatures at the lower limit of activity suggest the actual temperature below which there can be no trail activity. The range in these two temperatures at the upper limit of activity was much more variable. The results may suggest that neither of these temperatures influenced the morning cessation and afternoon initiation of trail activity. However, a number of supplementary factors must be taken into consideration. The temperature variation in the surface layer of air during periods of direct insolation is very great and consequently the ambient temperatures that influence the ant are extremely difficult to measure.

It was observed that when the higher temperature limits were approached the ants travelled largely in areas of shade afforded by low growing plants and along small sticks or straws that elevated them slightly above the soil surface. A series of 20 temperature readings with a movable thermocouple showed that the variation in such areas immediately before the morning cessation of trail activity was 51 degrees Fahrenheit. The fact that a large ant may stand approximately 1/4 inch high further complicates the determination of its ambient temperature. Table I shows that the temperature gradient between ground surface and 1/4 inch above the ground is often large. The body of the ant may be subjected to this entire range in temperature. Hence the averages between the temperatures at ground level and 1/4 inch above the ground were calculated. These averages give more consistent temperature data for the periods concerned and therefore are considered to represent the conditions affecting the ants to a greater extent than either temperature considered alone.



These variations in temperature together with the mobility of the ants make accurate determination of the temperatures influencing the ants almost impossible when using stationary thermocouples. The temperature obtained by use of the thermocouples should, however, possess a relationship to the ambient temperatures experienced by the ants.

To this point only the ambient temperatures recorded by thermocouples have been considered. It is the body temperature of the insect that ultimately governs its activity and under certain circumstances this may be very different from the ambient temperature. The morning start and evening stop of trail activity always occurred before sunrise or after sunset. At these times the ambient temperatures were relatively uniform because solar radiation did not influence them directly. Only evaporation and metabolic heat would serve to vary the body temperatures of the ants from ambient temperatures. Because these sources of variation are small and counteract one another (UVAROV, 1931; PARRY, 1951) they are not considered important in determining activity. This is supported by the relative uniformity of temperature data recorded for these periods.

During the high threshold period a very different situation existed. The ants and the surface thermocouples at this time were exposed directly to solar radiation and numerous differences in the temperatures of each occurred. As previously discussed, the mobility of the ants and the lack of mobility of the thermocouples account for many of the differences. In this respect, the direction of ant travel also influences the heating effect of solar radiation. An ant travelling at right angles to the incoming radiation exposes more heating surface than one travelling parallel to that radiation (UVAROV, 1948).

During periods of insolation the colour and shape of the ant also play a part in influencing its body temperature. The red and black colouration of *F. subnitens* would cause a greater absorption of heat than the light coloured sand used as a background for the thermocouples. Because of the curvature of the body of the ant some portion of it would receive solar radiation at right angles regardless of the position of the sun. In the latitude where these observations were made (50°N), solar radiation was never at right angles to the horizontal sand surface beneath the thermocouples, and hence never attained its full heating force on them.

In the final stage of activity during these periods of high temperature the ants dashed quickly from one shaded area to another, and often paused for several minutes in each. UVAROV (1948) showed that there is a slight lag in body temperature when an insect is exposed to solar radiation or when it is shaded from solar radiation. In ants, because of their small size, this lag would not be long, but the observations made indicate that it is of sufficient duration to allow the ants to dash from shaded area to shaded area when continuous solar heating would normally cause body temperatures too high for activity.

RELATIVE HUMIDITY.—The relative humidities given in Table I were obtained at the same distance above the ground as the standard air temperatures and hence, like them, had no direct influence on the ants. Nevertheless relative humidity taken at this level has a relationship with the relative humidity at ground level (GEIGER, 1950), so that, though no actual value for ground level relative humidity can be given, general relationships can be discussed.

From approximately 8.00 p.m. to 10.00 a.m. the relative humidity at ground level was higher than that 42 inches above the ground and the reverse was true from approximately 10.00 a.m. to 8.00 p.m. Table I shows that during the morning start of trail activity the relative humidity was never below 80 per cent. Considering the relative humidity relationships at this time (4.00 a.m. to 6.00 a.m.), it may be assumed that the relative humidity at ground level was even nearer saturation. This assumption is supported by the fact that there was usually dew during this period. Saturated air would almost prevent evaporation from the ant, which further increases the likelihood that the body temperature of the ant was near the ambient temperature during this threshold period of trail activity, as the extremely slow movements of the ant also minimized increases in body temperature by metabolism.

A similar situation existed at the time of the evening stop of activity. Though the relative humidities were lower during this period than in the morning period they were still sufficiently high to curb high evaporation from the body of the ant.

The morning stop of trail activity, judged from Geiger's relative humidity distribution graph, occurred when the humidities at ground level and at 42 inches above the ground were nearly equal. The afternoon threshold of trail activity occurred when the humidity at ground level was much lower than at 42 inches above the ground and was close to the minimum for the day. Similarity in the temperature ranges for the two periods would suggest that the humidity within the ranges considered was of little importance in limiting ant activity.

ATMOSPHERIC PRESSURE.—The sudden drop in atmospheric pressure that precedes a thunderstorm was associated with a marked increase in ant activity. However, such a drop occurred on only one occasion during threshold studies and, because this was accompanied by an increase in both temperature and relative humidity, little can be said regarding the effect of atmospheric pressure alone.

The actual level of atmospheric pressure did not appear to be related in any way to the thresholds of activity.

LIGHT.—Under field conditions light intensity is positively correlated with temperature and hence its effects on the start and stop of trail activity are difficult to evaluate. The variation in light intensity that occurred during the morning start, and particularly the difference in



light intensity between the morning start and evening stop, indicate that light has little effect in initiating or limiting activity. Such was found to be true in laboratory studies where temperatures and humidities were kept constant and light was allowed to follow its daily course. The light intensity had a marked influence on the level of activity but extremes did not cause cessation.

CLOUD.—Cloud cover did not appear to influence directly the start or stop of trail activity. The indirect influence of cloud was through the reduction of direct solar radiation which caused a lowering of temperatures during periods when high thresholds occurred. Thus, on overcast days, no halts in trail activity occurred. As solar heating was not involved in the morning start and evening stop periods, cloud cover at these times had no apparent effect on activity.

### *Fluctuations in foraging activities.*

TEMPERATURE.—In the preceding discussion it was concluded that standard air temperature and nest temperature did not have any direct effect on the start and stop of ant activity. For the same reasons given in that discussion these two temperatures had little effect on the daily course of ant activity and they will not be discussed further.

The data for temperature 1/4 inch above the ground showed that trail activity increased from the morning zero at 50.8°F. to a maximum at an average of 72.8°F., and then decreased to the morning stop at 94.7°F. In the afternoon period of activity the numbers of ants active increased from zero at 100.9°F. to a maximum at an average of 85.7°F., and then decreased to the evening zero at 46.5°F. The data for soil surface temperature showed similar trends: maximum activity occurred at average soil surface temperatures of 82.1° and 93.5°F. for morning and afternoon periods respectively.

As in the records for start and stop of trail activity, the average between the soil surface temperature and the temperature 1/4 inch above the ground is considered more representative of the temperature affecting the level of activity of the ants than either of those temperatures alone. The averages of these two temperatures gave seasonal averages of 77.8° and 90.1°F. for the morning and afternoon periods of maximum activity respectively.

RELATIVE HUMIDITY.—As previously stated, no measure of relative humidity at ground level was obtained. As relative humidity varies with temperature and as temperature variations at ground level are great during periods of insolation, the humidity readings 42 inches above the ground are of little significance. The relative humidity at ground level, however, would be less in the afternoon than in the morning and

this, in part, may account for the fact that maximum activity occurred at a higher temperature in the afternoon than in the morning.

ATMOSPHERIC PRESSURE, LIGHT, AND CLOUD.—Atmospheric pressure, light, and cloud are interrelated and in addition have direct or indirect effects on temperature and relative humidity. For this reason little can be said regarding their individual effects on the level of ant activity.

### *Area and types of foraging.*

The percentages of foraging ants on the four trails during all study periods throughout the season are shown in Table II. The percentages of the total foraging area served by the four foraging trails (fig. 1)

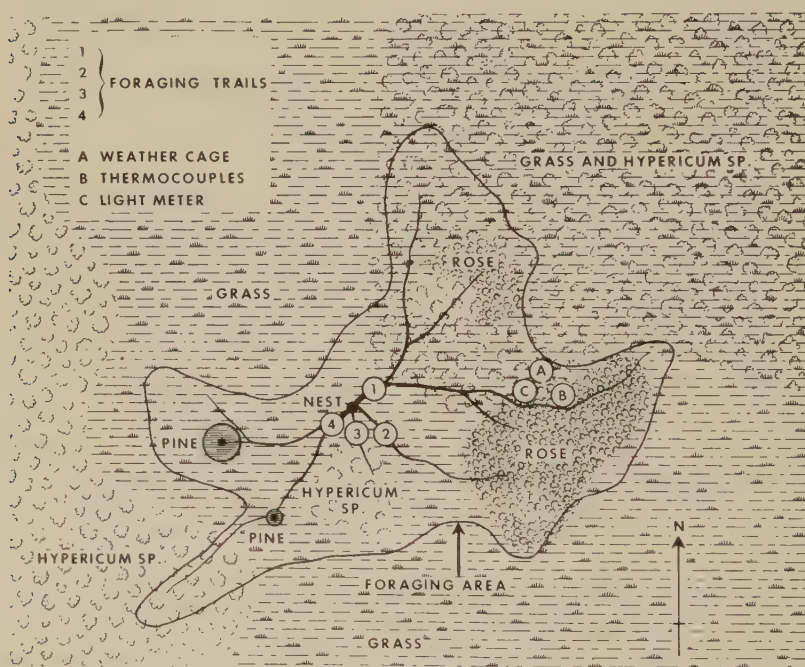


FIG. 1. — Map of a nest of *F. subnitens* and the foraging area showing the predominant types of vegetation, Westbank, B. C.

were approximately 48, 15, five and 32 respectively. As might be expected, the percentage of ants on each trail was of approximately the same order of magnitude as the percentage of total area served by the trail. The slight differences in percentages of the ants on trails one and two in relation to the percentages of foraging area served by these trails are believed caused by differences in the availability of food; the availability of food in each varied with the season.

TABLE II. — PERCENTAGES OF FORAGING ANTS ON THE FOUR TRAILS AT 8 A.M. AND 4 P.M. AT FORTNIGHTLY INTERVALS FROM MAY TO AUGUST, 1955\*.

DATE	TRAIL	8 A.M.	4 P.M.	TOTAL	DATE	TRAIL	8 A.M.	4 P.M.	TOTAL
<i>May 12</i>	1	33	40	37	<i>July 20</i>	1	46	37	44
	2	14	11	12		2	31	14	27
	3	11	13	12		3	3	3	3
	4	42	36	39		4	20	46	26
<i>May 26</i>	1	28	34	32	<i>Aug. 4.</i>	1	43	36	42
	2	7	6	7		2	46	32	43
	3	4	8	6		3	1	5	3
	4	61	52	55		4	10	27	12
<i>June 9.</i>	1	46	21	36	<i>Aug. 17</i>	1	43	38	41
	2	9	5	8		2	46	22	38
	3	8	5	7		3	2	4	3
	4	37	69	49		4	9	36	18
<i>July 6.</i>	1	52	43	47	<i>Aug. 30</i>	1	37	45	40
	2	23	15	19		2	50	23	40
	3	4	4	4		3	1	3	2
	4	21	38	30		4	12	29	18
TOTAL..						1	40	38	40
						2	30	15	23
						3	5	6	5
						4	25	41	32

The seasonal averages for food intake per trail reflected the productivity of the area served by the trail: over 80 per cent of all insect food brought to the nest was obtained on trails one and four whereas approximately 95 per cent of all insect secretions brought to the nest were obtained from trails one and two. Further breakdown of the data shows that trails one and two were the main sources of insects and insect secretions respectively.

The data collected for the seasonal changes in ant activity are too lengthy to give in full here. Data collected at 4.00 a.m., 12 noon, and 8.00 p.m. are omitted as variation in the times of start and stop of ant activity prevented gathering a complete set of data for these periods.

Field observations indicated that the areas of grass were more favourable for ant foraging in the spring and areas of bushes were more favourable in the fall. This change in preference for type of foraging area is shown by the increase in activity on trail two and the decrease in activity on trails three and four over the five-month period of study. A similar change of foraging areas occurred on trail one, but as this trail served areas of both types of vegetation the change was not shown in the data for total trail activity.

The cause of the change in preference for type of foraging area was twofold. The availability of food was probably of prime importance.



The increase in activity on trail two coincided with the growth of aphid populations on the rose bushes of the area. The increase in the aphid population was also accompanied by a decrease in abundance of insects in the grass areas because of the maturing and drying of the grass. This resulted in a decrease in activity on trails three and four. As stated previously, a similar situation existed on trail one but the methods of obtaining the data did not indicate the change.

The change in favoured foraging area was also related to the effects of microclimate on the ants. Though *F. subnitens* requires relatively warm temperatures for maximum activity, the areas of grass became too hot and dry for it towards the latter part of summer. The shade provided by low bushes gave more optimum meteorological conditions for ant activity during the latter part of summer than did the open grass areas.

The most notable daily variation in trail activity was the reversal in the magnitude of activity on trails two and four for the morning and afternoon periods after May 26. The cause of this fluctuation is unknown but the fact that the period of high activity always occurred when the ants on the trail concerned were moving toward the sun's compass position when they left the nest may be of significance. The percentages of ants on trails one and three did not change from morning to afternoon. Trail one led in a northerly direction and hence the ants, after leaving the nest, never travelled toward the compass point of the sun. If the direction of ant travel was influenced by polarized light, as found by VOWLES (1950), then variation similar to that on trail four should have occurred on trail two as the two trails were opposite and hence the plane of polarized light would be the same for both (WELLINGTON, 1951). Trail three, on the other hand, faced directly south and at both morning and afternoon periods the angle between the trail and the compass point of the sun was the same. At solar noon, when ants leaving the nest on this trail would have faced the sun's compass point, the ants were always inactive so that no data could be obtained for this period.

The possible influence of the compass position of the sun on the direction of ant travel is further illustrated by the data obtained for May 12 and 26. On these two days the reversal in magnitude of numbers of ants on trails two and four during morning and afternoon periods did not occur. These were the only days on which the sky was completely covered by cloud.

### Summary.

At Westbank, British Columbia, temperatures at and near the soil surface had a notable effect on the foraging activities of *Formica subnitens* Creighton; maximum activity occurred at average soil surface temperatures of 82.1° and 93.5°F. for morning and afternoon periods respectively. Relative humidity apparently influenced foraging activity but

the methods used for recording data proved unsatisfactory. Evidence that light and atmospheric pressure influenced foraging activities was obtained, but as changes in these factors were associated with changes in temperatures and relative humidity the effects of each were not determined. Evidence was also obtained that the direction of ant travel was influenced to some extent by the compass position of the sun.

### Résumé.

A Westbank (Colombie Britannique), les températures au sol et au voisinage de la surface du sol affectent les activités de récolte de *Formica subnitens* Creighton ; le maximum d'activité se produit lorsque la température moyenne de la surface du sol est de 82,1° F. le matin et 93,5° F. l'après-midi. L'humidité relative influe apparemment sur l'activité de récolte, mais les méthodes employées pour la mesure systématique de ses variations ne furent pas satisfaisantes. Il est évident que la luminosité et la pression atmosphérique influent sur les activités de récolte ; mais, comme les variations de ces facteurs s'accompagnent de variations de température et d'humidité relative, ce qui revient à chacun n'a pas été déterminé. On a pu montrer également que la direction du déplacement des Fourmis était influencée par la position astronomique du soleil.

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# VISUAL SENSITIVITY AND FORAGING IN SOCIAL WASPS

by

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## INTRODUCTION

A substantial amount of experimental work has been concerned with the properties of the compound eye of insects, particularly of honey-bees. Most such studies are either of visual sensitivity, or of brightness or colour discrimination of flying insects, but only when these are sessile and working at the lower limit of their sensitivity. Little attention has been paid to the possibility that functional threshold illuminations for a flying insect in actual flight may be substantially higher than for a sessile insect. The luminosity thresholds for the cat ( $1 \times 10^8$  millelamberts) and for man ( $5.5 \times 10^7$  mL.) as determined by GUNTER (1951), provide local illuminations much below that at which these mammals are able to negotiate objects at speed.

WOLF and ZERRAHN-WOLF (1936) find that the eye of the honey-bee, light-adapted at 142 mL. failed to respond to a moving strip pattern at luminosities equivalent to 1-2 mL. After some 30 min. dark adaptation, the strip pattern could be detected at about  $2 \times 10^3$  mL. BARLOW (1952) has suggested that, in order to be continuously visible to a honey-bee, a barely distinguishable mark must be subjected to at least a thousand times the illumination necessary for human sight to distinguish it. BARLOW also showed that the sensitivity of the hymenopterous eye was approximately proportional to the length of the eye, so that larger insects should be the more sensitive.

The sensitivity of the hymenopterous eye as a whole seems to depend on the largest number of ommatidia aligned in any one direction (the length of the eye being the greatest such distance) provided that the interommatidial angle is kept just below the limiting resolving power of each ommatidium. Evidently, such a limitation restricts the number of facets in an eye of a given size. Barlow discusses the possible advantages to an insect of increasing either of these competing attributes. TEISSIER (1926) had earlier found that, over a wide range of insects including the Vespinae, the allometric growth of the insects is such that the surface area of a facet is proportional to the number of ommatidia in an eye. This relationship presumably reflects the optimum balance between the two desiderata noted above. Since this relation holds even among the different instars of the mainly nocturnal *Blatta orientalis* L. it is unlikely to be a characteristic of diurnal insects alone, though there are specialized insects for which this relation may not hold. The nocturnally foraging South American wasp *Ipocia* has smaller eyes than have Vespinae, but the shape of the eye is different and the ocelli are more developed (RICHARDS and RICHARDS, 1951). Differences in the foraging periods of social hymenoptera may be related to their visual sensitivities. The hornet for instance, continues to forage in moonlight (WOOD, 1872) whereas the writer knows of no such records for British wasps. The object of this paper is to present the evidence which establishes the relation between the duration of foraging activity and functional visual sensitivity, on a quantitative basis, for some of the social hymenoptera.

## EXPERIMENTAL

Records of the horizontal illumination were taken at dusk, or at dawn, when foraging ceased or commenced. The first practical difficulty was to establish the end-points of activity. The second was to decide whether to record the luminosity of the nest entrance and flight markers, often in shade, or the general horizontal illumination in the open. Neither difficulty proved severe.

Two end-points were found to be reproducibly observable at dusk: the refusal of potential foragers to leave the nest, and the return of the last forager. Refusal to forage was usually preceded by abortive flight just sufficiently far from the nest for the worker to obtain a clear view of the sky. When perhaps half a dozen such flights had resulted in the workers hesitating, and returning to the nest, no further sorties were observed. The manner in which these decisions were made by the workers determined the choice of horizontal illumination as a measure of light intensity rather than nest luminosity.

Exception might be taken to the recording of the illuminations when the last forager returns, on the grounds that, once sorties have ceased, the normal duration of a foraging trip will decide what illumination obtains when the last entry is made. This duration would, stochastically, tend to increase with the number of foragers out at the time. However, there is evidence that worker wasps do not always return to the nest at night (GAUL, 1952; BLACKITH, 1957) though how general this tendency may be is not clear. The last workers at the nest entrance fly slowly from one minor reference mark, such as a twig or leaf, to another, and collisions with leaves or blades of grass or with other workers are common. This behaviour, together with the sudden cessation of activity at a clearly defined level of illumination, leaves little doubt that the last entrants are flying at the effective limit of their visual sensitivity. There are interesting specific differences in the behaviour of wasps trying to locate the nest entrance at dusk. *V. rufa* hovers until it can lower itself into the hole, but *V. germanica* lands impetuously near the nest and half crawls, half flies, to the hole. *V. vulgaris* resembles *V. germanica* in this respect.

When this behaviour was seen, a reading was rapidly taken with a "Lumeter" photometer. By pre-setting the instrument to the expected range, and keeping it as near the nest as the shading effect of trees, etc. permitted, only a few seconds elapsed before attention was again transferred to the nest to ensure that activity had ceased. The low reflectivity coefficient of nest entrances is noteworthy; it usually lies between 0.1 and 0.05.

The identification of the wasps was in each instance confirmed by excavating the nests and extracting the males and females at the end of the season.

## RESULTS

Two facts support the contention that illumination is by far the most important single factor in determining the duration of foraging in the Vespinae. One of these facts is the close agreement between the foraging thresholds at dawn and at dusk.

When considering this agreement the normal range of diurnal variation is worth bearing in mind. Full summer sunlight provides some 8-10,000 lumens/sq.ft., whereas a starlit but moonless night provides about 0.002 lumens/sq.ft. Within this wide range we find that, for *V. germanica* (Nest A) in Table I, the mean illumination at dawn for the first sortie is 0.15 lumens/sq.ft. and in the evening the last forager returns when the illumination falls to 0.25 lumens/sq.ft.



TABLE I.—*V. germanica*.

DATE.	NEST.	AIR TEMP. °C.	ILLUMINATION (LUMENS/SQ. FT.) AT			WEATHER NOTES.
			<i>First sortie.</i>	<i>Last sortie.</i>	<i>Last entry.</i>	
—	—	—	—	—	—	—
5 ix '55	A	16.1	—	5.78	0.21	Clear skies after rain.
6 ix '55	A	15.0	—	2.89	0.35	Clear skies.
7 ix '55	A	6.1/16.7	0.18	1.73	0.30	Clear skies, dawn and dusk, mist at dawn.
8 ix '55	A	17.2	—	2.60	0.35	Clear skies.
9 ix '55	A	12.8/13.6	0.17	3.32	0.36	Clear skies dawn and dusk.
13 ix '55	A	11.1/10.6	0.14	8.08	0.36	Heavy cloud, rain at dawn.
14 ix '55	A	7.8	0.21	—	—	Clear skies.
16 ix '55	A	13.3	—	2.02	0.19	Heavy cloud.
26 ix '55	A	12.2	—	6.91	0.23	Light cloud.
30 ix '55	A	13.3	0.12	—	—	Cloudy.
6 x '55	A	11.1/11.1	0.11	1.77	0.24	Light cloud, strong winds dawn and dusk.
11 x '55	A	15.6	—	2.26	0.12	Light cloud.
14 x '55	A	11.7	—	2.74	0.09	Clear skies.

TABLE II.—*V. rufa*.

DATE.	NEST.	AIR TEMP. °C.	ILLUMINATION (LUMENS/SQ. FT.) AT			WEATHER NOTES.
			<i>First sortie.</i>	<i>Last sortie.</i>	<i>Last entry.</i>	
—	—	—	—	—	—	—
31 vii '52	B	17.8	—	2.20	0.19	Broken cloud
6 viii '52	B	12.8/17.2	0.12	1.39	0.28	Thin cloud dawn; thick cloud dusk, after rain.
24 viii '55	C	13.3/22.2	0.40	5.78	0.78	Cloudy dawn and dusk; light mist dawn.
26 viii '55	C	18.9	—	2.02	0.72	—
29 viii '55	C	15.6	—	4.04	0.86	Clear skies.
30 viii '55	C	18.3	—	3.17	0.37	—
1 ix '55	C	12.2/20.0	0.60	2.02	0.26	Clear skies dawn; cloudy dusk.
2 ix '55	C	16.1	—	6.37	0.99	—

TABLE III.—*V. vulgaris*.

DATE.	NEST.	AIR TEMP. °C.	ILLUMINATION (LUMENS/SQ. FT.) AT		
			<i>First sortie.</i>	<i>Last sortie.</i>	<i>Last entry.</i>
—	—	—	—	—	—
13 viii '52	D	17.2	—	4.00	0.39
14 viii '52	D	15.6	—	1.38	0.35
15 viii '53	E	15.4	—	1.33	0.17
19 viii '53	F	15.4	—	2.50	0.30
21 viii '53	G	11.7	—	0.95	0.12
24 viii '53	G	14.4	—	1.50	0.13
26 viii '53	G	13.9	—	1.33	0.20
27 viii '53	G	14.4	—	1.17	0.12

TABLE IV.—*V. crabro*.

DATE.	NEST.	AIR TEMP. °C.	ILLUMINATION (LUMENS/SQ. FT.) AT		
			<i>First sortie.</i>	<i>Last sortie.</i>	<i>Last entry.</i>
—	—	—	—	—	—
14 viii '53	H	13.3	—	0.0133	0.0033
21 viii '53	H	12.2	—	0.0130	0.0025
24 viii '53	H	14.4	—	0.0160	0.0042
26 viii '53	H	10.6/10.6	0.010	0.0180	0.0020
27 viii '53	H	13.3	—	0.0150	0.0017

Secondly, when the illumination approaches the threshold in the evening, the workers are plainly flying at the limit of their visual sensitivity. Typically, they collide with one another and with twigs, leaves, and blades of grass and navigate to the nest by way of a series of minor reference marks which are not searched for during the day even though the wasps may in fact be using them as reference points.

Similarly, for hornets (table IV) there is good agreement between the illumination at which they refuse to forage and that at which they recommence foraging. These insects, apparently, do not need to refrain from leaving the nest at an illumination higher than their visual threshold, as do wasps, because their visual threshold is so much lower. For large hymenoptera, the foraging thresholds lie within ranges of illumination at which predicted dark-adaptation should be complete, in the hornet this range corresponds roughly with that found on a moonlit night. Direct observation, both visual and aural, confirms the continued nocturnal foraging of hornets recorded by Wood (1872). If a cloud passes across the moon, foraging is suspended and restored with the moonlight, suggesting that changes of illumination are readily discovered by the workers. Moreover, these thresholds are much the same whether the moon is full, but lightly obscured by cloud (a diffuse source), or whether it is only three quarters full (virtually a point source).



There is now good evidence that the function of the workers stationed at night near the nest entrance is more closely connected with the perception of light intensity than with defence. Negative evidence is that such workers are often so cold after a few hours in this position that they are capable only of clumsy movements, such as a feeble hostile separation of the mandible when prodded and they fail to respond to a suspended live worker from another nest. Nevertheless, shortly before the foraging threshold illumination is reached at dawn, these workers crawl out to the platform of bare earth and excavated particles common round wasps nests and then back into the nest. The inference that the onset of foraging is prepared by the return of the workers, often loosely regarded as sentries, seems reasonable, though no doubt the information conveyed is no more specific than generalized activity. On only one occasion has a foreign insect been observed to enter a nest. At first light on 11.X.'55 a flying *Geotrupes stercorarius* landed on the entrance of the *V. germanica* nest, and half walked, half fell, inside. The workers at the entrance made no response other than the usual swaying of the body which can be evoked by prodding them with a stick. Not until the beetle had been in the nest for about a minute was there any demonstration by the wasps, but the noise of the eventual disturbance was considerable, though no wasps left the nest during it. When this nest was excavated a week later the dismembered integument of the beetle was found below the nest. Badgers, too, seem able to excavate wasps' nests at night with impunity, although the eyes and nose are exposed to stings. A noticeable feature of the activity of badgers at Silwood Park, where 7 of the 9 known nests were destroyed by them during 1955, is that nests of more than about 3-500 workers are rarely attacked. Several workers have pointed out that wasps in larger nests become more aggressive than those in less populous nests.

### *Changes of apparent threshold values with number of foraging insects.*

The difficulty of defining a threshold in terms of the behaviour of the first or last insect to perform an action is that the vagaries of an individual are substituted for the average behaviour of a group of insects. Nevertheless, these vagaries are themselves predictable. Generally, the more workers there are foraging the sharper will these thresholds be defined. Although we know that the sorties from, and entries to, a nest follow the negative binomial distribution, we may consider the low foraging densities for which the frequencies become indistinguishable from the Poisson expectations (Blackith, 1957). It is for such low frequencies that the problem of estimating the thresholds becomes most acute.

If there are  $m$  wasps returning to the nest per minute at dusk, the probability that the minute in which the true threshold illumination is attained will have no returning foragers is  $e^{-m}$ . Thus on  $1/e^m$  of the evenings on which

the last returning forager is watched, the estimated threshold will be too high by the amount by which the illumination is deteriorating per minute. Similarly, one out of every  $e^{2m}$  evenings will give estimates which are high by an amount equivalent to the deterioration of illumination during the two-minute interval. Under normal conditions, this deterioration is about 0.2 lumen/sq.ft. in two minutes. A more accurate, though less immediately useful, estimate is that the illumination decreases by a factor of 10 in 10-15 minutes. Broken cloud will produce substantial divergencies from this rate over short periods.

We can obtain some estimate of the error thus caused by considering a nest whose foragers return at the low rate of one a minute.

On an average one threshold in every three will be high by some 0.2 lumens/sq.ft. Such a bias will be much reduced by an increase of foraging strength.

### *Relation between eye sizes and foraging thresholds.*

The simple relation propounded by Barlow (1952), that the sensitivity of the hymenopterous eye is likely to be proportional to its length, needs qualification in the present context. Barlow's examples of social wasps include measurements of the eye of a queen *V. germanica* (as evidenced by the length of 3.31 mm. plotted in his figure) and a queen of *V. crabro* (plotted eye-length 4.60 mm.). For our discussion we need the lengths of eye for workers. Moreover, some idea of the distribution of these lengths of eye is useful, because, if the range is wide and the distribution skew, an unrepresentative minority of workers may be concerned with those first sorties or last entries which determine the thresholds.

The eyelengths of 330 workers of *V. germanica* (from nest A; Table I) were found to have a mean of 2.478 mm. The standard error of the distribution was 0.13 mm. and that of the mean was 0.0070 mm. The distribution was symmetrical and showed no tendency to log-normality. The range was narrow from 2.2 to 2.8 mm. The possibility still exists that the late foragers are a biased sample of the worker force, but the importance of this possibility is much diminished. The mean length of 50 eyes from the virgin queens of this nest was 3.176 mm. (standard error of a distribution; 0.087 mm., and of the mean 0.012 mm.). The notably greater uniformity of the queens is in accordance with the experience of THOMSON, BELL and PEARSON (1910). The eyes of 100 *V. vulgaris* workers were on an average 2.337 mm. long, with standard errors of 0.096 mm. for the distribution and 0.009 mm. for the mean. Thus there is a significant discrepancy of eyelength between these two sets of workers of the two species. However, the proper sampling unit for investigations of social wasps is probably the nest rather than the individual, so that much more extensive investigation would be required

before one could say more than that the difference in size of the eyes is negligibly small for the present discussion.

Similarly, two samples of workers were taken from two different nests of *V. rufa*. Nest C (Table II) produced workers whose mean eye—length was 2.445 mm., with standard errors of 0.057 for the mean of 35 wasps, 0.315 for the distribution. Another nest not included in the tables contained workers with eyes averaging 2.366 mm. the standard errors being 0.094 for the distribution, and 0.014 for the mean of 41 individuals. The mean lengths of eye from each nest differ significantly at the 5 % level of probability, confirming the suggestion of THOMSON, BELL and PEARSON (1910) and of RICHARDS and RICHARDS (1951) that the effective sampling unit for social wasps is the nest rather than the individual.

The length of the eye of a stock of honeybees was 2.052 mm. (standard error of mean of 50 workers 0.018) a value substantially lower than that for wasps. Worker hornets, on the other hand, have eyes of average length 3.933 mm. with a standard error of 0.088 for the mean of 4 measured workers. Thus hornets, wasps and honey-bees have clearly different lengths of eye, and clearly different functional illumination thresholds, which are inversely related to the eye-lengths.

## DISCUSSION

The outstanding conclusion from these experiments is that the level of illumination is at once important and different in kind from the other factors which influence foraging activity. Adverse factors other than low illumination, such as coldness, high winds, or heavy rain, may each reduce the number of workers foraging, but they do not alter the diurnal limits of this activity save in so far as these depend stochastically on the number of foragers.

Otherwise, a few workers will leave the nest at dawn even when the grass temperatures are as low as 2°C, or in winds gusting to Force 7 (about 50 km./hr.) on the Beaufort scale (moderate gale) and in steady rain. The readiness of workers to leave the nest under such conditions seems greater at dawn (first light) than at any other time.

The processes of nest-awakening, taking flight, and foraging are distinct. The first two processes are uniquely determined by the illumination, though adverse conditions may induce a high proportion of workers to refuse to forage, and at dusk the foragers will refuse at illuminations insufficient to permit the successful conclusion of a sortie. Foraging itself depends on the visibility of reference marks, and is shown to be distinct from, though naturally bound up with, illumination by the behaviour of workers in a thick mist at dawn. In these circumstances the worker will take flight as soon as the critical illumination is reached, but wander in the vicinity of the nest before returning, for a period which increases as the visibility improves. In terms of the human eye, a visibility



of about 70 yds. is needed for free foraging without refusals, but the difference between human and vespine vision may well vitiate this comparison.

The compound structure of the insect eye might lead one to expect a different threshold according to whether the illumination is diffuse or concentrated. Yet the intensity of illumination required for the foraging of hornets is the same whether it be from a full moon lightly obscured by cloud or an unobscured three-quarter moon. The behaviour of workers whose nest is among undergrowth supports the view that wasps judge when to take flight by the appearance of the sky, and are not misled by artificial (local) illumination. Such workers fly as far as is necessary to obtain a clear view of the sky, though such short trips are often observed in unobscured nests, even when no refuse is to be dropped, at dusk.

The decision to refuse or to continue foraging must depend on the sensitivity of the individual worker, but is also likely to vary with the drive to a particular form of collecting activity. BRIAN and BRIAN (1953) have shown that the predominant form of foraging activity alters during the day, and that workers engaged on one activity are but little interested in opportunities for other types of foraging. Since these drives are probably acquired during the worker's stay in the nest, their willingness to forage may be modified by the extent to which environmental conditions interfere with the several forms of activity. A forager intending to collect insect food might well be more easily deterred by low temperatures than would be one requiring building material or concerned to jettison refuse.

A noticeable feature of wasp behaviour is the greater élan with which wasps move at dawn, perhaps because the light is then improving, perhaps because they are then rested. Workers take rapid advantage of lulls in periods of inclement weather, arriving back at the nest during intervals between showers and gusts of wind where possible.

Although the main conclusions of this work are in broad agreement with those of GAUL (1952) the amplification of the scope of the work suggests that revision of his conclusions is desirable. GAUL suggests that, up to a point, higher temperatures induce activity at lower intensities of illumination, and conversely. The difference between the species studied by GAUL and those studied here may account for the present conclusion that activity is independent of temperature above 20°C, but it is also possible that GAUL made insufficient allowance for the quantitative relationship between temperature and activity, and hence the indirect stochastic dependence of the illumination threshold on the ambient temperature, without there being any direct qualitative dependence.

According to GAUL, the lowest temperature at which *Vespula maculifrons* Bey will fly is 8.5°C, and for *Dolichovespula maculata* L. it is 5°C. These values seem to be higher than for any British species of *Vespula*, whose thresholds lie between 0.1 and 1.0 lumens per sq. ft. at all temperature down to 2°C. If we ignore the supposed influence of temperature in

GAUL's experiments, his species fly at illuminations within the range quoted for the European species.

The ecological consequences of these physiological differences among Vespinae are considerable. The worker force of the hornet has, potentially, a foraging capacity out of all proportion to the numerical relation between the numbers of workers severally available to hornets and to those wasps with subterranean nests. Taking the foraging threshold at 0.01 lumens/sq.ft. there will be some 20 nights during the season throughout which hornets can forage, weather permitting. A full moon provides an illumination of about 0.013 lumens/sq.ft. and in general not all the night will be so illuminated. We do not know, however, whether rest is necessary for the workers, nor whether all types of foraging can be done at these low illuminations.

Nests of social wasps kept in the laboratory and made visible by removal of the envelope show greatly reduced activity at night. Some indication that this result is not an artefact of captivity is given by the rapid nocturnal killing of wild nests with hydrogen cyanide. On excavation some workers are found with larvae and small stones or earth in their mandibles, which fact suggests some continued activity at night.

The worker force normally increases up to the time the sexual forms are produced, but the amount of work which can be done by each worker outside the nest decreases steadily from midsummer, when about 17 hours are light enough for wasps to work, until early November, when only about 10 hours can be worked. This reduction of the effective foraging capacity is more serious for wasps than for hornets.

A few observations on honey-bees suggest that although the critical illuminations are much higher for *Apis* than for wasps, the difference between the logarithmic intensities at which sorties and entries cease is the same as it is for wasps and for hornets. This constant difference in stimulus, measured on that logarithmic scale which is appropriate to many biological stimuli, suggests that the higher illumination needed for sorties by social hymenoptera at dusk may be determined by a difference in the drive to foraging rather than by the teleologically more obvious need to allow time for a forage before return to the nest becomes impracticable. However, the drive of the honey-bee towards foraging activity is notoriously dependent on the weather, and on the honey-flow, so that this part of the investigation was not pursued.

### *Summary.*

While there is a distinction between that intensity of illumination which permits social wasps to forage, and that to which a sessile worker can respond, nevertheless illumination is the most critical of the environmental factors which control the activity of wasps. Low temperatures, high winds, and heavy rain all reduce activity but unless exceptionally

severe do not wholly stop it. At dawn, when the critical level of illumination is attained, workers leave the nest, but at dusk they will not leave should the same critical level be due in the course of the foraging flight, after which they could not return.

The three species of wasp, *Vespula vulgaris*, *V. rufa*, and *V. germanica* have a common threshold of illumination, although the hornet, *Vespa crabro* can forage in moonlight at an altogether lower illumination. Honey-bees normally need a still higher illumination than do wasps.

In all these species, the thresholds of illumination are related to the length of the compound eyes, so that species with large eyes need less light by which to forage. Moreover, there is a slight difference between the threshold at dawn when workers leave the nest, and that at dusk, when they must needs have sufficient light by which to return. This difference is almost constant for each species, when, as is customary, one measures it on a logarithmic scale.

Lastly, the estimates, which these experiments provide, of the threshold illuminations depend stochastically on the number of workers foraging. A correction for this bias is given.

### Sommaire.

Parmi les facteurs du milieu qui contrôlent l'activité des guêpes, celui de l'intensité de lumière est le plus important ; toutefois on note une différence entre l'intensité de lumière qui permet aux guêpes sociales de fourrager, et celle qui produit une réponse des ouvrières sessiles.

En général, les basses températures, les vents forts, et les grandes pluies réduisent leur activité, mais ces facteurs ne l'arrêtent pas complètement, à moins qu'ils ne soient très marqués.

A l'aube, quand le niveau critique de lumière est atteint, les ouvrières quittent le guêpier, mais, le soir, si elles s'attendent à ce que la lumière vienne à s'abaisser au cours de leur sortie au-dessous du niveau critique, elles ne sortent pas.

Les trois espèces de guêpe, *Vespula vulgaris*, *V. rufa*, et *V. germanica*, réagissent au même seuil de lumière, mais le frelon, *Vespa crabro*, est capable de fourrager au clair de lune par une lumière moins intense. Normalement, les abeilles exigent une lumière plus intense que les guêpes.

Dans toutes ces espèces, le seuil de lumière se rapporte à la hauteur des yeux composés, par conséquent les espèces pourvues de grands yeux sont à même de fourrager par une lumière moins intense. De plus, il y a une légère différence entre le seuil de lumière à l'aube, quand les ouvrières quittent le guêpier, et celui du soir lorsqu'elles ont besoin d'une lumière suffisante pour rentrer. Cette différence, quand elle est mesurée à l'échelle logarithmique, comme il est d'usage, est presque constante pour chaque espèce.

Enfin, les évaluations du seuil de lumière dans ces expériences dépendent stochastiquement du nombre d'ouvrières en train de fourrager. On a tenu compte de ce fait.



*Epitome.*

Distinctio inter duas res fit, aut lumen idoneum est qui vespis socialibus facultatem volitare det, aut stativas vespas utcunque ututque respondere sinet. Si lux tenet, et frigus et ventus atque imber strenuitatem vesparum aegre opprimunt, nisi quum graviore sunt; sin minus, obscuritas immobilitatem importat.

Tria genera, id est *Vespula vulgaris*, *V. rufa*, *V. germanica*, supparibus liminibus lucis expergiscuntur proveniuntque, sed de crabrone, *Vespa crabro*, propter oculos longiores vespis lumen minus est, quoad lunae lumen desit. Contrarie, de apibus in alveum congerens propter oculos breviores limen superat.

Prima luce limen lucis subtiliter sed significanter deficit quod ad crepusculum attinet dum lux paulatim contabescit. Disjunctio inter haec limina in unoquoque genere constat, dummodo ad gradum logarithmeticum, ut est consuetudo, disponantur. Vesperi vespae, omissa fuga, temperi commorantur, quominus permulti pabulatores, quasi in loco clarigationis, abnoctent.

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# CONTRIBUTION A L'ÉTUDE DE L'ONTOGENÈSE SENSORI-NERVEUSE DU TERMITE *CALOTERMES FLAVICOLLIS* FAB.

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## Introduction.

L'anatomie sensori-nerveuse des Termites est encore mal connue. Les travaux de HARTWELL (1924) se rapportent à *Reticulitermes flavipes*, ceux de NOYES (1929) à *Termopsis angusticollis* Hagen et ceux de RICHARD à *Calotermes flavicollis* Fab. Ce dernier auteur a étudié, en particulier, les pattes (1949-1950) et les pièces buccales (1951) de la nymphe du septième stade de développement.

J'ai repris l'étude de l'anatomie sensori-nerveuse des pattes de *Calotermes flavicollis* Fab., en précisant plus spécialement la mise en place des nerfs et des sensilles au cours de l'ontogenèse de cet Insecte paurométabole.

## Matériel et méthodes.

*Calotermes flavicollis* Fab. (super-ordre des Blattoptéroïdes, ordre des Isoptères, famille des Calotermitidae) vit dans le Midi de la France. Ses colonies se développent principalement dans les troncs de Micocouliers et dans les ceps de vigne. Les animaux étudiés ont été récoltés à Banyuls-sur-Mer.

Pour colorer les nerfs et les cellules nerveuses, j'ai utilisé la méthode de coloration supra-vitale au bleu de méthylène. Le bleu est celui de GURR (Londres) en solution à 1 % dans une solution de chlorure de sodium à 0,75 %. Selon la méthode mise au point par RICHARD (1950), le bleu est injecté dans les pattes, à l'aide d'une pipette de verre, et fixé par le molybdate d'ammonium en solution aqueuse à 1 % pendant douze heures à la glacière. Ensuite les pièces sont lavées deux heures dans l'eau courante, déshydratées rapidement dans l'alcool absolu, éclaircies dans le toluène et montées *in toto* entre lame et lamelle dans le baume du Canada. Cette méthode colore électivement le tissu nerveux.

L'orientation des pattes est donnée par la convention de GRIMSHAW (1908) : les membres étendus perpendiculairement à l'axe longitudinal du corps présentent une face dorsale, une face ventrale et des faces latérales, antérieure et postérieure.

## Caractérisation des stades de développement.

Les stades larvaires successifs ont été déterminés par des mesures du coxa, du fémur et du tibia (tableau I). Par ailleurs, les nymphes ont été également caractérisées par le développement de leurs fourreaux alaires et la formation des ébauches oculaires. Les nymphes du cinquième



stade ont des fourreaux alaires très courts, celles du sixième stade ont des fourreaux plus grands. Au septième stade, les fourreaux alaires sont très allongés et les ébauches oculaires se pigmentent chez les individus âgés.

TABLEAU I. — DIMENSIONS DU COXA, DU FÉMUR ET DU TIBIA DES LARVES ET DE L'IMAGO.

(Les dimensions sont exprimées en microns.)

STADES	COXA		FÉMUR		TIBIA	
	Longueur	Largeur	Longueur	Largeur	Longueur	Largeur
1	200	170	260	90	260	50
2	220	180	300	100	300	60
3	280	190	360	130	360	80
4	390	250	480	160	480	110
5	600	480	670	230	670	150
6	670	540	690	230	690	150
7	750	600	720	240	720	160
Imago	840	670	750	250	750	160

### TOPOGRAPHIE SENSORI-NERVEUSE AU COURS DU DÉVELOPPEMENT LARVAIRE

1. — **Généralités.** — Les pattes de *Calotermes flavicollis* Fab. portent de nombreux organes sensoriels se rattachant à deux grandes catégories (RICHARD, 1949 et 1950) : ce sont, d'une part, les sensilles externes chitinisées réparties sur toute la surface des pattes, d'autre part les organes chordotonaux, organes sensoriels internes, dont l'extrémité est constituée par une substance sans doute légèrement différente de la cuticule chitineuse. Ces derniers peuvent être isolés ou groupés, constituant alors des complexes chordotonaux.

Les sensilles externes sont de trois sortes (terminologie de SNODGRASS) : Les *sensilla trichodea* ; ce sont des soies coniques à longueur de beaucoup supérieure au diamètre de base, mais dont la taille est variable. Elles sont réparties sur l'ensemble de la patte. — Les *sensilla basiconica* ; ce sont aussi des soies coniques, mais dont la longueur est peu supérieure au diamètre de base ; leurs parois sont moins épaisses que celles des

*sensilla trichodea*. Elles se présentent en groupes situés à des endroits fixes. Elles sont toutes de taille égale chez des larves d'âge déterminé. — Les *sensilla campaniformia*, ou pores sensoriels (ou pores de HICKS) ; ces sensilles ont une forme circulaire ou elliptique et on distingue : des pores de grandes dimensions souvent groupés et toujours situés à des places fixes ; des pores de petites dimensions répartis sur l'ensemble de la patte.

Les *sensilla trichodea* des larves de *Calotermes* appartenant aux quatre premiers stades de développement ont des dimensions relativement peu variables (tableau II).

TABLEAU II. — DIMENSIONS DES ORGANES SENSORIELS DE LA PATTE DES DIVERSES LARVES ET DE L'IMAGO AU COURS DU DÉVELOPPEMENT.  
(Les dimensions sont exprimées en microns.)

STADES	SENSILLA TRICHODEA		S. BASICONICA		S. CAMPANIFORMIA	
	Longueur	Diamètre de base	Longueur	Diamètre de base	Gdes S.c. grand/petit diamètre	Ptes S.c. grand/petit diamètre
1	25 à 35	3 à 4	8	1,5	5/4	
2	<i>Id.</i>	<i>Id.</i>	<i>Id.</i>	<i>Id.</i>	<i>Id.</i>	
3	25 à 40	<i>Id.</i>	10	<i>Id.</i>	<i>Id.</i>	4/3
4	<i>Id.</i>	<i>Id.</i>	15	2	<i>Id.</i>	<i>Id.</i>
5	8 à 15	1,5 à 2	20	3,5	6/5	5/4
	25 à 35	3 à 4				
	40 à 60	5 à 6				
6 et 7	<i>Id.</i>	<i>Id.</i>	<i>Id.</i>	<i>Id.</i>	<i>Id.</i>	<i>Id.</i>
Imago	10 à 25	2 à 3	30	4	8/6	6/4
	40 à 60	5				
	70 à 80	8				
	120 à 140	8				

Mais, chez les nymphes et chez les imagos, on peut reconnaître des sensilles de trois tailles.

REMARQUE. — Quelle que soit la dimension ou la position d'une sensille, elle est, en général, innervée par une seule cellule sensorielle dont le noyau a un diamètre de 10 à 12 microns. Seules certaines grosses *sensilla campaniformia* ont une cellule sensorielle dont le diamètre du noyau atteint 15 microns.

2. — **Les organes sensoriels de la larve néonate.** — Je décrirai la patte mésothoracique, qui représente le type moyen. La patte prothoracique présente quelques variations par rapport à ce type moyen ; ces variations seront soulignées plus loin.

a) COXA. — Le côté dorsal de la face antérieure du coxa est marqué par une dépression longitudinale. Cette face porte dorsalement sur son bord proximal un groupe de 4 ou 5 *sensilla basiconica* et, ventralement, 1 ou 2 *sensilla trichodea*. Dans la région médio-dorsale, s'échelonnent 4 ou 5 *sensilla trichodea* ; une dernière est située dans la région ventrale.

La face postérieure porte 3 ou 4 *sensilla trichodea* le long du bord dorsal, puis une autre ventralement. (Fig. 1)

b) TROCHANTER. — Près de l'articulation coxo-trochantérale, et en position dorsale sur la face antérieure, se place un groupe de 5 ou 6 *sensilla basiconica*. Au centre de cette face, on trouve deux groupes de 3 à 4 *sensilla campaniformia*, et un autre de trois le long du bord distal. La face antérieure porte encore une *sensilla trichodea* en position dorsale et trois autres en position ventrale. Enfin on remarque 2 petites sensilles (8 microns) situées sur le bord ventral, près de l'articulation coxo-trochantérale.

La face postérieure porte en son centre un groupe de 4 *sensilla campaniformia*, et un autre groupe plus ventral de 3 *sensilla trichodea*.

c) FÉMUR. — Le bord dorsal de la face antérieure porte une rangée de 5 ou 6 *sensilla trichodea*, le bord ventral n'en porte que 2 ou 3. Une autre sensille est située au milieu et plus distalement.

Dans la région proximale de la face postérieure on relève 2 *sensilla campaniformia*. Le bord dorsal porte 4 ou 5 *sensilla trichodea* alignées ; le bord ventral n'en porte qu'une ; on relève une autre *sensilla trichodea* au centre de l'article et 2 à son bord distal.

Six clous scolopaux sont groupés dorsalement dans le fémur et une dizaine d'autres sont échelonnés jusque dans la région médiane de l'article : ils constituent le scoloparium fémoral.

d) TIBIA. — Au tiers proximal du tibia, et dorsalement sur la face postérieure, on voit 2 *sensilla campaniformia* (pores de Hicks).

Distalement sur la face antérieure se trouvent les ébauches de 2 petites



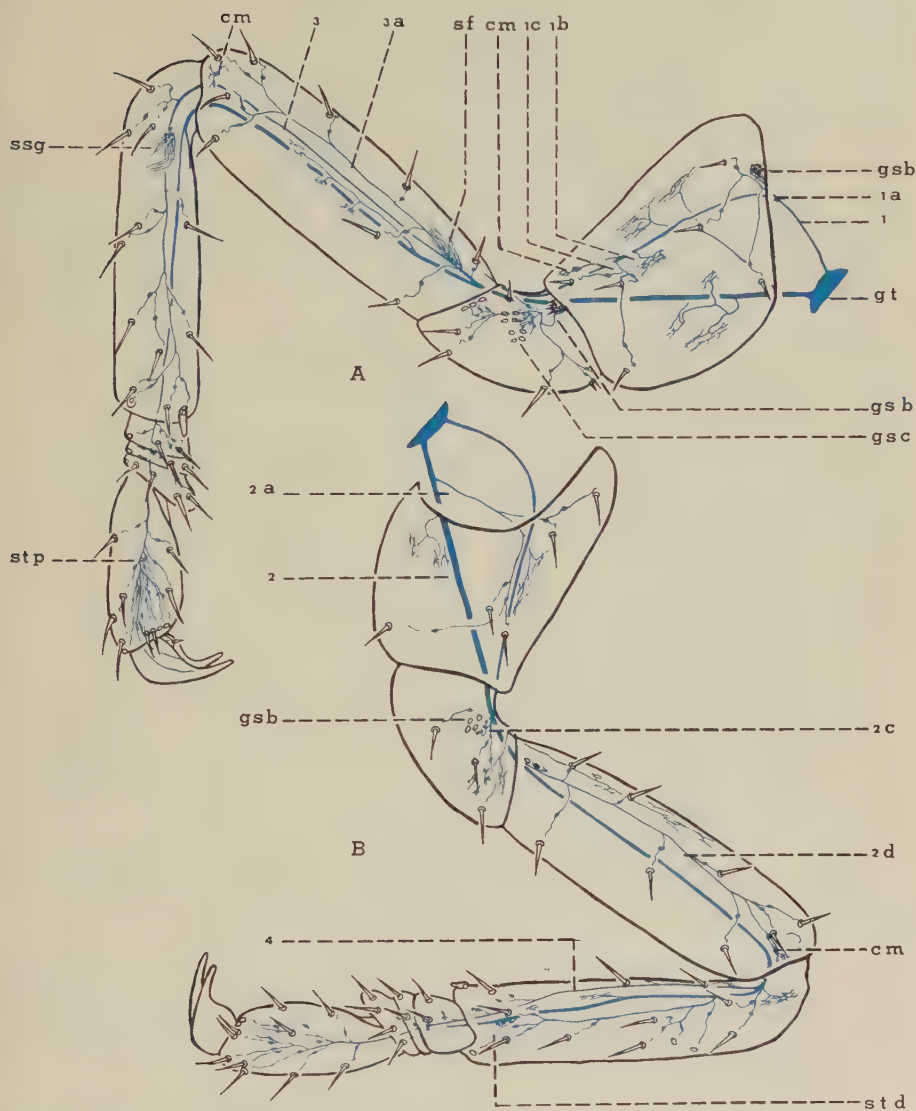


FIG. 1. — Patte mésothoracique de la larve néonate de *Calotermes flavicollis*. Organes sensoriels. Nerfs sensoriels et nerfs moteurs.

A, face antérieure ; B, face postérieure,  $\times 110$  ; gt, ganglion thoracique ; cm, cellule multipolaire ; gsb, groupe de sensilla basiconica ; gsc, groupe de sensilla campaniformia ; sf, scoloparium fémoral ; ssg, scoloparium subgénéral ; std, scoloparium tibial distal ; stp, scoloparium tarso-prétarsien ; 1, nerf antérieur ventral ; 2, nerf postérieur ventral ; 3, nerf tibial antérieur ; 4, nerf postérieur.

épines avec un pore à leur base. L'une est ventrale, l'autre dorsale. En position analogue, la face postérieure porte l'ébauche d'une épine ventrale avec son pore basal, et un pore dorsal.

Sur la face antérieure du tibia, on voit 3 ou 4 *sensilla trichodea* sur le bord dorsal, 2 sur le bord ventral et 5 dans la partie médiane.

Sur la face postérieure, on voit 3 ou 4 *sensilla trichodea* sur le bord dorsal, 3 sur le bord ventral et 3 ou 4 médialement.

Le scoloparium subgénual situé au tiers proximal, dans le conduit sanguin dorsal du tibia, contient 7 clous scolopaux. Il comprend un organe subgénual proprement dit à 4 clous scolopaux en direction transversale et un subgénual distal à 3 clous scolopaux en direction oblique. Distalement, dans le conduit sanguin dorsal du tibia, 3 clous scolopaux groupés constituent le scoloparium tibial distal. Chacune des 3 petites épines tibiales présente également un clou scolopal dans sa base.

e) TARSE. — Sur la face antérieure, chacun des deux premiers articles du tarse porte 2 *sensilla trichodea*, l'une ventrale, l'autre dorsale. Le troisième article a 4 sensilles, 2 ventrales, une médiane et une dorsale.

Le prétarse porte 3 ou 4 *sensilla trichodea* dorsalement sur la face antérieure, 2 ventralement et 4 dans la région médiane.

La face postérieure du tarse montre la même topographie sensorielle que la face antérieure.

Chaque article du tarse porte dorsalement, en outre, une *sensilla campaniformia*.

Le bord articulaire distal du prétarse montre un pore dorsal entre les deux griffes et 2 pores ventraux sur chaque face. Ces pores sont situés à proximité de 2 *sensilla trichodea*. Entre les deux griffes se trouve une petite *sensilla trichodea* (8 microns).

Dans le prétarse, on relève 3 clous scolopaux constituant le scoloparium tarso-prétarsien et deux autres dont les prolongements distaux pénètrent dans les deux griffes.

3. — **Les nerfs de la larve néonate.** — Du ganglion thoracique partent deux nerfs qui pénètrent dans le coxa et vont innerver les muscles et les organes sensoriels de la patte : ce sont le *nerf antérieur ventral* (nerf 1) et le *nerf postérieur ventral* (nerf 2).

a) LE NERF ANTÉRIEUR VENTRAL. — Le nerf antérieur ventral naît latéralement du ganglion thoracique et presque en position dorsale. De ce nerf se détache rapidement une branche tégumentaire qui innerve les sensilles du sternite au voisinage de l'articulation coxale. Puis le nerf 1 pénètre ventralement dans le coxa et le traverse en position antéro-dorsale, les rameaux sensoriels qu'il fournit s'épanouissent sous la face antérieure du coxa. Dès son entrée dans cet article, il émet une branche (1 a) dont un rameau court innerve la plaque de *sensilla basiconica* située dans la région proximale. Un second nerf plus long fournit 2 ou 3 terminaisons

sensorielles dans la région médio-dorsale. Une deuxième branche (1 *b*), très courte, issue du nerf 1, est motrice : ses prolongements se perdent dans un des faisceaux du muscle élévateur du trochanter. Une troisième branche (1 *c*) sensorielle envoie 2 ou 3 terminaisons distalement et ventralement. Dans le coxa enfin, le nerf 1 envoie un petit rameau terminé par une cellule multipolaire située dorsalement près de l'articulation coxo-trochantérale. Le nerf 1 pénètre dans le trochanter et le traverse en position dorsale. Distalement, dans cet article, il fournit un rameau moteur dont les terminaisons se perdent dans les muscles réducteurs du fémur. Il pénètre enfin dans le fémur, où il se termine dans les muscles éleveurs du tibia.

*b*) LE NERF POSTÉRIEUR VENTRAL. — Il est beaucoup plus gros et plus important que le précédent, et il atteint l'extrémité du tarse. Il naît latéralement du ganglion et en position presque ventrale. Il émet rapidement une branche importante (2 *a*) dont un premier rameau est moteur. Il innerve les muscles pleuro-tergaux du coxa, les muscles rotateurs antérieurs et les muscles abducteurs du coxa, ainsi que tous les muscles éleveurs et dépresseurs thoraciques du trochanter. Un second rameau est sensoriel, il se bifurque rapidement. L'une de ses branches fournit 2 ou 3 terminaisons dans la partie proximale dorsale de la face postérieure du coxa. L'autre, plus importante, envoie deux prolongements dorsaux et un ventral. Un dernier rameau issu du nerf (2 *a*) innerve les muscles rotateurs postérieurs du coxa et le muscle abducteur du même article. Distalement, le nerf 2 envoie un rameau moteur dans les muscles dépresseurs du trochanter. Le nerf 2 pénètre dans le trochanter en position dorsale, il fournit alors deux branches sensorielles. L'une (2 *b*) s'épanouit vers la face antérieure. Dès sa naissance, elle se divise en quatre rameaux dont le premier innerve le groupe de *sensilla basiconica*. Le second se dirige vers la région proximale ventrale, où il fournit trois prolongements. Le troisième innerve les deux groupes centraux de *sensilla campaniformia*. Le dernier se dirige vers la région distale, où il innerve les *sensilla campaniformia* situées le long de l'articulation trochantéro-fémorale ; il se prolonge obliquement par deux terminaisons. L'autre branche (2 *c*) issue du nerf 2 dans le trochanter a une origine très voisine de celle du nerf (2 *b*), elle s'épanouit sous la face postérieure. Elle se divise dès sa naissance en trois parties. Un prolongement se dirige vers la région ventrale. Un rameau très court fournit des arborisations vers le groupe de *sensilla campaniformia*. Un dernier rameau part obliquement et envoie deux terminaisons dans la partie distale du trochanter.

Le nerf 2 traverse dorsalement le trochanter, mais toujours en position ventrale par rapport au nerf 1. Contrairement à ce qu'a observé DEBAISIEUX chez les Blattes, ces deux nerfs ne se fusionnent pas dans cet article ; dans certains cas, toutefois, ils semblent se chevaucher.

Le nerf 2 pénètre ensuite dans le fémur. Il émet aussitôt une branche très importante, le nerf tibial antérieur (nerf 3), qui, dès son individuali-



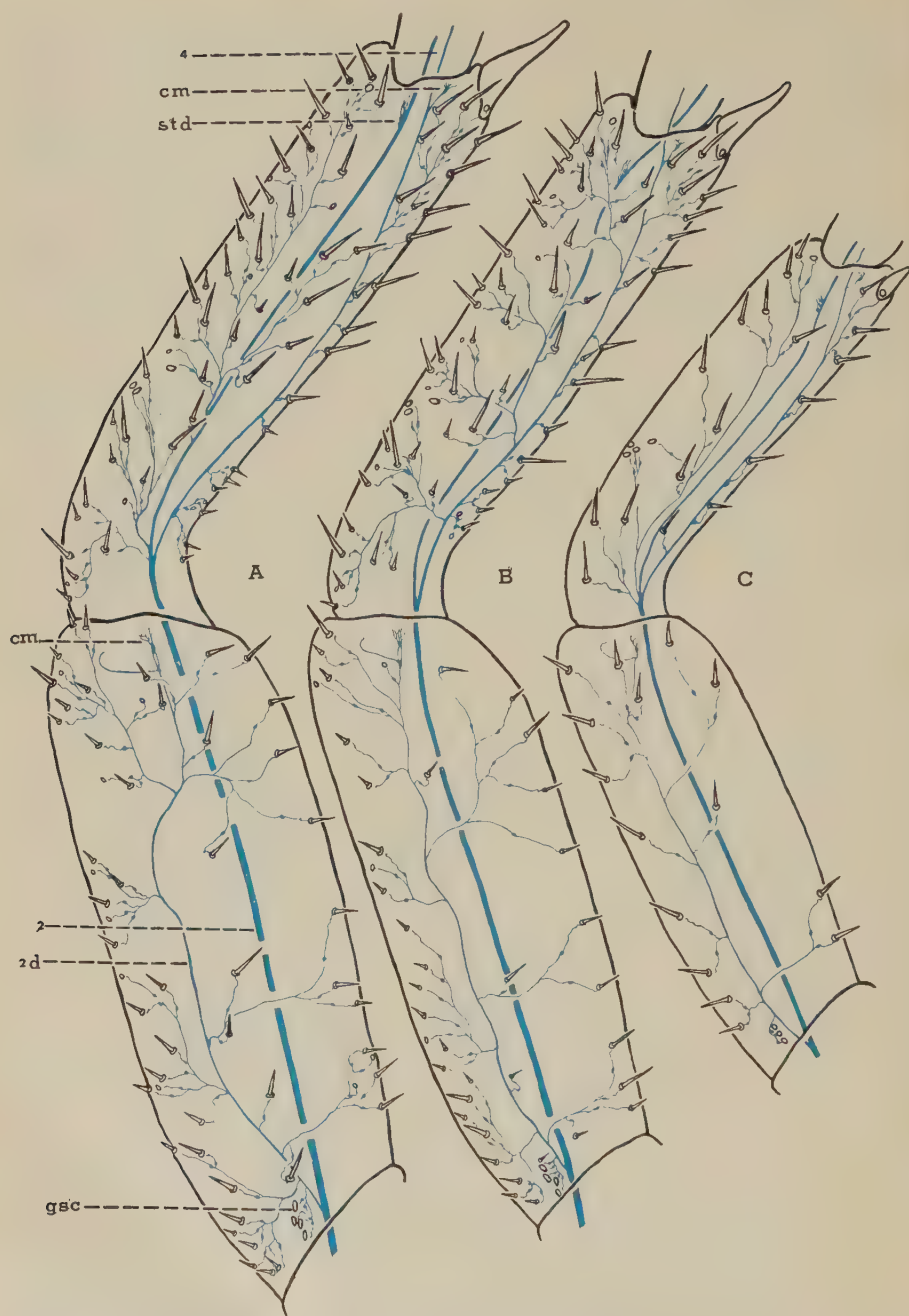


FIG. 2. — Fémur et tibia. Face antérieure. Évolution des organes sensoriels et des nerfs sensoriels au cours du développement larvaire.

A, larve du septième stade ; B, larve du cinquième stade ; C, larve du troisième stade ; A et B,  $\times 75$  ; C,  $\times 110$  ; *cm*, cellule multipolaire ; *sf*, scoloparium fémoral ; *ssg*, scoloparium subgénéral ; 2, nerf postérieur ventral ; 3, nerf tibial antérieur ; 4, nerf tibial postérieur.

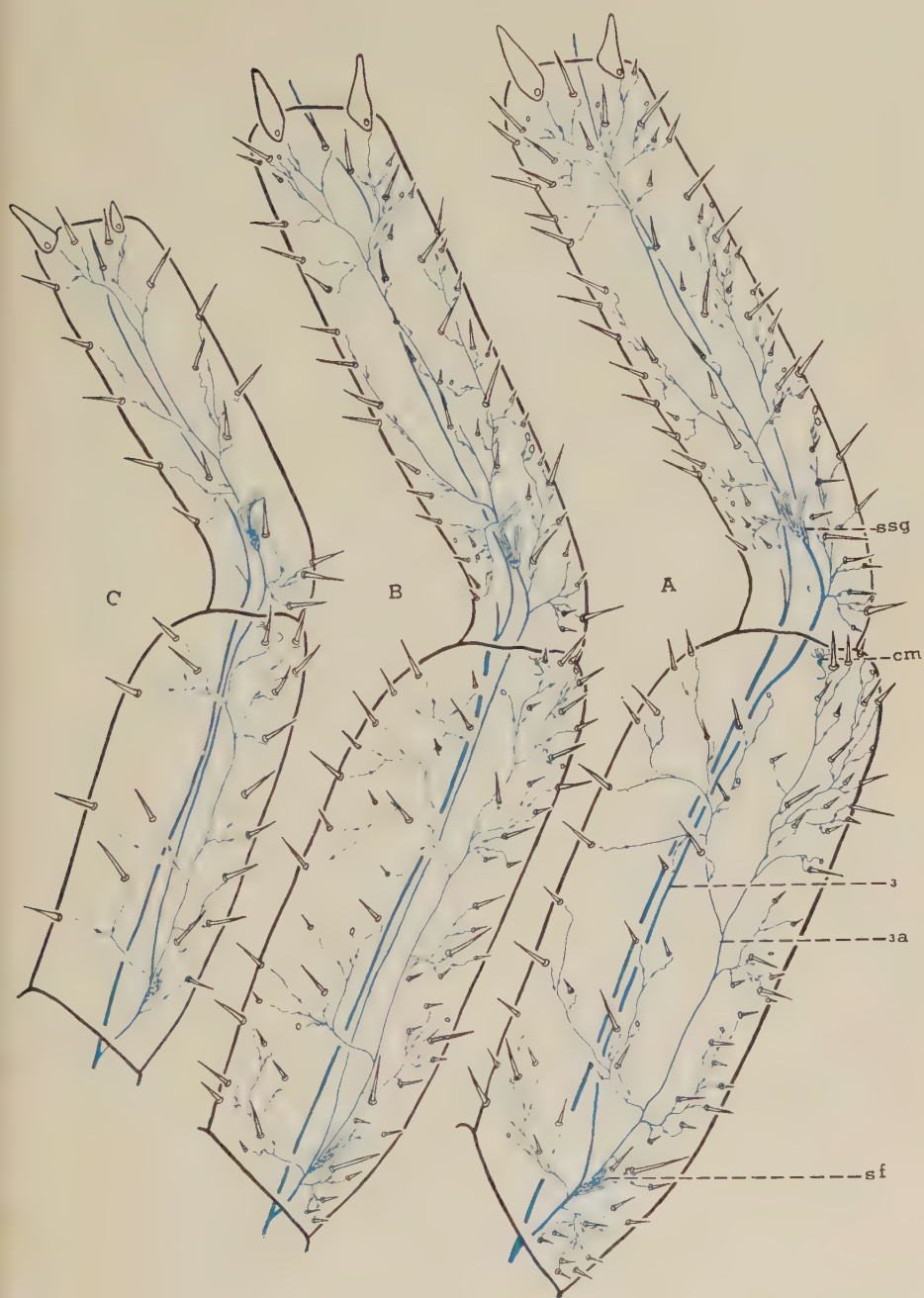


FIG. 3. — Fémur et tibia. Face postérieure.

sation, envoie deux prolongements sensoriels, l'un ventral, l'autre dorsal. Puis le nerf 3 se divise en donnant une branche sensorielle (3 *a*), ou nerf fémoral antérieur, qui innerve le scoloparium fémoral et poursuit son trajet en position antéro-dorsale jusqu'à l'extrémité du fémur, où elle se termine par 4 ou 5 arborisations sous la face antérieure. Sur son parcours, elle envoie aussi vers cette face un prolongement ventral et un dorsal.

Le nerf 3 traverse le fémur dans l'axe de cet article et pénètre dans le tibia où il se termine. Il fournit tout d'abord un petit rameau sensoriel proximal dans la région antéro-dorsale. Puis le nerf (3) innerve l'organe subgénéral et poursuit son trajet en position antérieure jusqu'à l'extrémité du tibia, où il se termine par 6 ou 7 arborisations innervant notamment les deux pores distaux. Sur son parcours il fournit aussi 3 ou 4 prolongements dans la région moyenne du tibia.

Tout près de l'origine du nerf 3, le nerf 2 émet une branche sensorielle (2 *d*) ou nerf fémoral postérieur, dont un petit rameau innerve le groupe de pores situés proximalelement sur la face postérieure. La branche (2 *d*) suit un trajet postéro-dorsal jusqu'à l'extrémité du fémur, où elle se termine en formant 3 ou 4 arborisations. Sur son parcours, elle envoie 4 ou 5 terminaisons ; 2 ou 3 se dirigent dorsalement et 2 ventralement. Distalement, elle forme un demi-collier autour de l'apodème dorsal du tibia, reliant ainsi deux cellules multipolaires dont les prolongements dendritiques se perdent dans l'articulation fémoro-tibiale.

Le nerf 2 traverse le fémur en position axiale comme le nerf 3, envoyant sur son parcours des rameaux moteurs aux muscles déprimeurs du tibia. Il pénètre ensuite dans cet article, où il donne naissance à une branche sensorielle importante : le nerf tibial postérieur (nerf 4).

Le nerf 2 reste profond ; il traverse le tibia en position médio-ventrale. Dans cet article, il fournit 3 rameaux moteurs, le premier est proximal et innerve le muscle déprimeur du prétarse, le second est médian et innerve le muscle élévateur du tarse, le dernier est émis au tiers distal et se rend au muscle déprimeur du tarse. Le nerf 2 passe ensuite en position axiale, innerve le scoloparium tibial distal et pénètre dans le tarse.

Il envoie 2 petits rameaux sensoriels en position antérieure dans les trois articles du tarse. Dans le prétarse, il fournit plusieurs terminaisons sensorielles en position antérieure, innervant notamment les deux pores ventraux et celui qui est situé dorsalement entre les deux griffes.

Le nerf 4 envoie une branche sensorielle postérieure dans la région proximale du tibia et innerve le pore de Hicks le moins éloigné. C'est un autre petit rameau issu du nerf 4 qui se rend au deuxième pore de Hicks. Le nerf 4 traverse le tibia en position postéro-ventrale, envoyant 2 ou 3 terminaisons sur son parcours. Il fournit, par contre, 4 ou 5 prolongements postéro-dorsaux plus longs. Distalement, un petit rameau innerve notamment le pore situé à la base de l'épine postéro-ventrale du tibia et le clou scolopal de celle-ci. Puis le nerf 4 passe en position axiale, envoie un prolongement à une cellule multipolaire située dans l'articula-



tion tibio-tarsienne et pénètre dans le tarse. Il émet alors 2 ou 3 petits rameaux sensoriels postérieurs dans les trois articles du tarse et innerve notamment les 3 pores situés dorsalement sur chacun des articles du tarse. Il se termine dans le prétarse en position postérieure, formant des arborisations sensorielles superficielles.

4. — **Ontogenèse sensorielle.** — Au cours des trois premières mues larvaires, le nombre des organes sensoriels augmente assez peu (tableau III) et la patte d'une larve du quatrième stade ressemble beaucoup à celle d'une larve néonate. Il se forme à chacune de ces mues 3 à 5 *sensilla trichodea* sur la face antérieure et sur la face postérieure de chacun des segments de la patte, excepté sur le trochanter. Les groupes de *sensilla basiconica* et de *sensilla campaniformia* situés sur le coxa, le trochanter, le fémur et le tibia comptent 1 ou 2 sensilles supplémentaires après chacune de ces mues. En particulier, à la première mue larvaire, il se forme sur le tibia 2 *sensilla campaniformia* situées dorsalement par rapport au pore de Hicks le plus proximal. Enfin, il se forme 1 à 3 petites *sensilla campaniformia* sur la face antérieure et la face postérieure de chacun des segments de la patte lors de la deuxième et de la troisième mue larvaire.

Chez les larves du quatrième stade de développement se produit un renflement de la partie dorsale du coxa. Ce renflement s'accroît chez les larves du cinquième stade. La dépression de la face antérieure subsiste et isole une partie dorsale sur cette face.

Les organes sensoriels subissent une forte multiplication au cours de la quatrième mue larvaire. On distingue alors des *sensilla trichodea* de tailles différentes (voir le tableau II).

Dès le cinquième stade larvaire, on peut définir des territoires de la patte sur lesquels la densité des organes sensoriels est plus ou moins forte. Sur le coxa, les régions ventrales antérieure et postérieure, ainsi que la région postéro-dorsale, sont riches en *sensilla trichodea*. La face antérieure du trochanter est particulièrement riche en organes sensoriels. Le fémur et le tibia présentent une forte densité de *sensilla trichodea* dorsalement sur leurs faces antérieure et postérieure, et à leur extrémité distale, près de l'articulation. De même, l'extrémité du prétarse est riche en organes sensoriels.

Les nymphes des sixième et septième stades montrent une augmentation du nombre des organes sensoriels. Toutefois, la densité relative des sensilles sur les territoires définis chez les nymphes du cinquième stade ne change pas.

Les organes sensoriels de l'imago sont sensiblement plus grands que ceux des nymphes ; certains peuvent atteindre la taille de 120 à 140 microns. L'arête dorsale du coxa est encore plus accentuée que chez les larves. Par contre, la topographie sensorielle de la patte de l'imago ressemble beaucoup à celle de la patte d'une nymphe, et les territoires particulièrement riches en organes sensoriels définis précédemment sont les mêmes.

REMARQUE. — Le nombre de clous scolopaux de chaque organe chondotonal reste constant au cours de l'évolution post-embryonnaire.

TABLEAU III. — NOMBRE TOTAL DE SENSILLES SUR LA FACE ANTÉRIEURE ET LA FACE POSTÉRIEURE DU COXA, DU FÉMUR ET DU TIBIA.

STADES	COXA		FÉMUR		TIBIA	
	<i>Face antérieure</i>	<i>Face postérieure</i>	<i>Face antérieure</i>	<i>Face postérieure</i>	<i>Face antérieure</i>	<i>Face postérieure</i>
1	10 à 12	4 à 5	9 à 10	10 à 11	12 à 13	14 à 15
5	110	60	70	45	65	70
Imago	150	90	100	85	80	85

*Individus du huitième stade.*

On sait que certains soldats de la colonie et que les pseudergates (GRASSÉ et NOIROT) sont issus des nymphes du septième stade après une mue supplémentaire régressive.

Il était intéressant de comparer leur chétotaxie à celle des autres individus de la colonie.

LES SOLDATS. — On ne remarque qu'un fort élargissement du fémur. (Le rapport entre la longueur et la largeur du fémur est de 2,5, alors qu'il est de 3 pour les larves et pour l'imago.) Le nombre et la taille des organes sensoriels restent les mêmes que chez les nymphes du septième stade.

LES PSEUDERGATES. — La protubérance dorsale du coxa est peu accentuée. Les segments de la patte sont plus grêles. Le rapport de la longueur à la largeur du fémur est de 3,5. On constate une forte régression du nombre des organes sensoriels sur la face postérieure du coxa et du fémur. Par contre, leur taille reste sensiblement la même que chez l'imago. La face postérieure du coxa porte une dizaine de sensilles de taille normale (50 à 70 microns) sur le bord proximal dorsal et autant sur le bord ventral. Au centre de cette face, on ne voit que 10 à 15 sensilles très petites (5 à 10 microns). La face antérieure du fémur porte 8 à 10 sensilles de grande taille ventralement. Ces grandes sensilles manquent d'ailleurs chez certains pseudergates examinés. Sur la face postérieure, par contre,

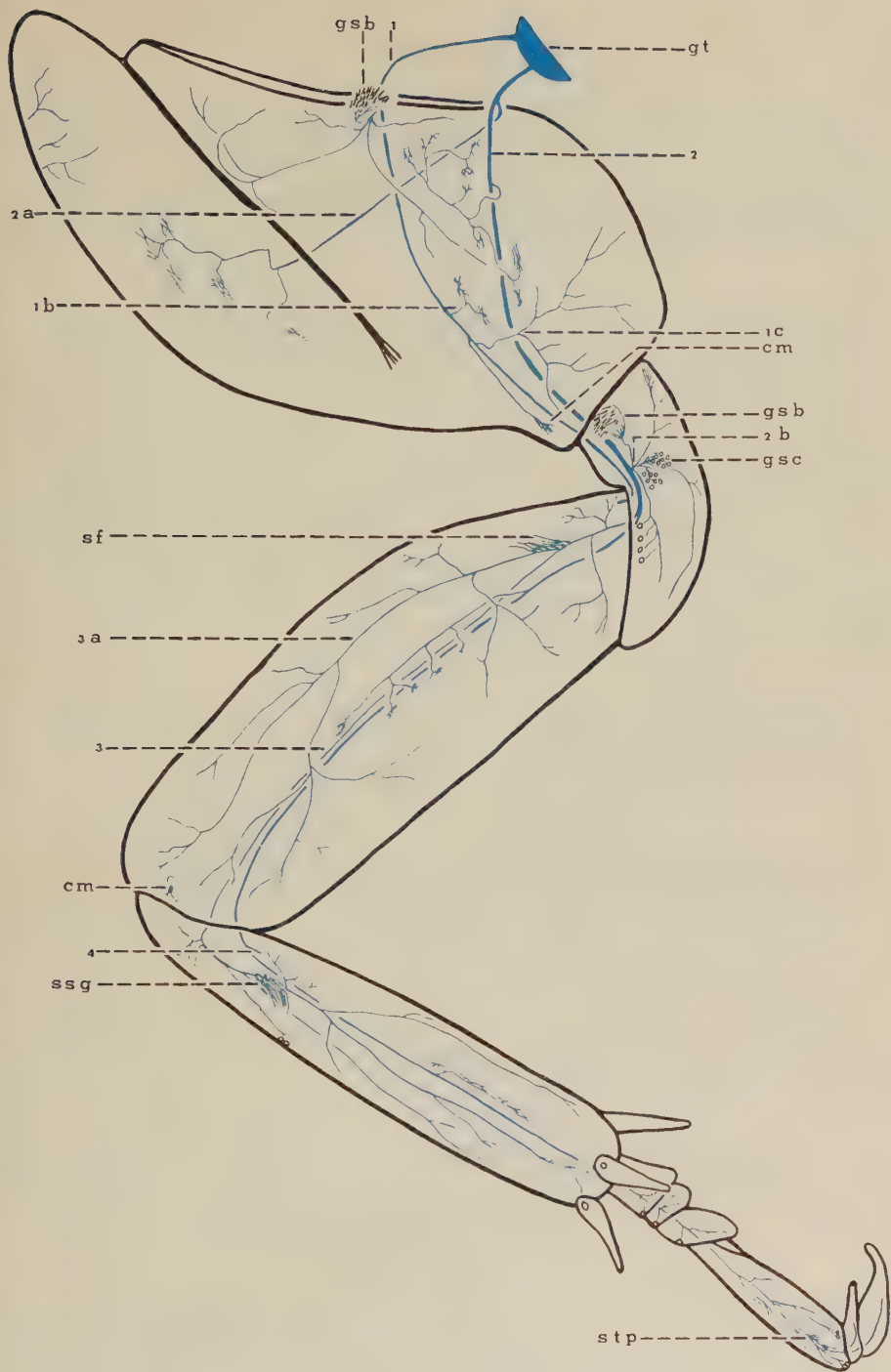


FIG. 4. — Patte mésothoracique de l'imago. Face antérieure.  $\times 60$ .

gt ganglion thoracique ; cm, cellule multipolaire ; gsb, groupe de sensilla basiconica ; gsc, groupe de sensilla campaniformia ; sf, scoloparium fémoral ; ssg, scoloparium subgénéral ; stp, scoloparium tarso-prétarsien ; 1, nerf antérieur ventral ; 2, nerf postérieur ventral ; 3, nerf tibial antérieur ; 4, nerf tibial postérieur.



on trouve une vingtaine de très petites sensilles (5 à 10 microns). Les deux groupes de *sensilla basiconica* du coxa et du trochanter ne comptent chacun que 5 à 7 sensilles. Chacun des groupes centraux de pores du trochanter n'a que 4 à 5 *sensilla campaniformia*. Il n'y a pas de régression sensible sur le tibia et sur le tarse.

*Comparaison de la patte métathoracique et de la patte mésothoracique.*

La patte métathoracique ressemble beaucoup à la patte mésothoracique. Les différences portent en particulier sur la taille du tibia : le tibia mésothoracique de la larve néonate mesure 250 microns, alors que le tibia métathoracique de la même mesure 280 microns. Au cours des mues, la croissance du tibia métathoracique est plus rapide que celle du tibia mésothoracique. Chez l'adulte, le tibia métathoracique mesure environ 1 000 microns et le tibia mésothoracique 750 microns. Le dénombrement des organes sensoriels sur les deux tibias met en évidence une différence de 20 % en faveur du tibia métathoracique.

*Comparaison de la patte prothoracique et de la patte mésothoracique.*

La patte prothoracique présente plusieurs particularités.

COXA. — La dépression dorsale signalée sur la face antérieure du coxa mésothoracique n'existe pas sur cette face, mais se retrouve sur la face postérieure. La partie dorsale est d'ailleurs moins volumineuse par rapport à l'ensemble du coxa. On trouve 75 à 80 sensilles sur la face antérieure et 65 à 70 sur la face postérieure, chez l'imago.

TROCHANTER. — La courbure de ce segment est moins accentuée que dans la patte mésothoracique, mais le nombre et la topographie des organes sensoriels ne changent pas.

FÉMUR. — Le nombre et la taille des organes sensoriels sont plus grands sur la face postérieure de cet article que sur l'autre face. On peut mettre en évidence une inversion antéro-postérieure de l'anatomie sensorielle de ce segment si on la compare aux fémurs méso- et métathoraciques.

TIBIA. — Le tibia prothoracique est toujours moins long que le tibia mésothoracique. La différence de longueur, peu accentuée chez les larves des premiers stades, devient importante chez les larves du cinquième stade, et le tibia prothoracique de l'imago mesure environ 630 microns. Le nombre des organes sensoriels est alors inférieur de 10 % à ce qu'il est sur le tibia mésothoracique mesurant 750 microns.

Distalement, sur la face antérieure du tibia prothoracique, on ne voit

qu'une épine ventrale. Les deux autres épines sont situées sur la face postérieure ; l'une est ventrale, l'autre est dorsale.

TARSE. — Seul, le premier article du tarse est moins long que l'article correspondant des tarses des deux autres pattes. Il porte alors deux fois moins de sensilles que ses homologues.

REMARQUE. — Les régressions déjà signalées sur la face postérieure des pattes mésothoraciques des pseudergates se retrouvent sur la même face de leurs pattes métathoraciques et sur la face antérieure de leurs pattes prothoraciques.

5. — **Ontogénèse nerveuse.** — Dans la patte de la larve néonate, les nerfs principaux, en position centrale, fournissent des terminaisons sensorielles isolées ou groupées par deux ou par trois. Au cours des premières mues larvaires, quelques cellules sensorielles apparaissent et il se forme des rameaux nerveux secondaires sur les nerfs principaux. Chez les larves du cinquième stade de développement, les nerfs principaux sont très gros et les rameaux secondaires forment de nombreuses arborisations. La bifurcation du nerf 1 a donné deux rameaux sensoriels, dont l'un s'épanouit médialement et l'autre dorsalement vers la face antérieure du coxa. Des branches sensorielles s'individualisent latéralement à partir du nerf (3 a) ; deux ou trois de ces branches se dirigent dorsalement et deux ventralement vers la face antérieure du fémur. Des branches nerveuses analogues se sont formées latéralement à partir du nerf (2 d) ; celles-ci sont moins ramifiées. Deux grands nerfs sensoriels antérieurs se sont individualisés à partir du nerf 3 ; l'un s'étend dans la région dorsale, l'autre dans la région ventrale du tibia. Des nerfs 2 ou 4 se détachent deux branches sensorielles postérieures qui se dirigent vers la partie dorsale du tibia. Distalement, les nerfs 2 et 4 se bifurquent dans le prétarse et fournissent de nombreuses arborisations.

Chez les larves des sixième et septième stades du développement, chez l'imago et chez les autres individus du huitième stade, l'anatomie nerveuse de la patte ne se modifie pas. Seules, les arborisations périphériques évoluent en rapport avec la multiplication déjà décrite des organes sensoriels.

#### *Variations individuelles du plan général d'innervation.*

Dans certains cas, la région ventrale du coxa est innervée par des arborisations sensorielles fournies par une branche nerveuse issue du nerf moteur qui innerve les muscles rotateurs postérieurs du coxa. Corrélativement au développement de ce nerf, les branches (1 c) et (2 a) sont plus courtes et se terminent dans la région médiane du coxa.

Dans le fémur, chacun des nerfs fémoraux antérieur et postérieur ne

donne, parfois, qu'un rameau dorsal et un rameau ventral innervant alors les parties proximale et médiane du fémur.

Dans le tibia, les rameaux sensoriels dorsaux diffèrent en nombre et en position. Ils sont issus du nerf 2 ou du nerf 4 et à des niveaux variables selon les individus.

Les prolongements sensoriels qui innervent les pores dorsaux des trois articles du tarse sont issus soit du nerf 2, soit du nerf 4.

### *Comparaison de la patte prothoracique et de la patte mésothoracique.*

La seule variation importante du plan d'innervation de la patte prothoracique par rapport à la patte métathoracique se remarque dans le coxa, où le nerf 1 ne fournit qu'un rameau sensoriel (1 *a*). C'est ce rameau qui innerve l'ensemble de la face antérieure et le nerf 1 *c* n'existe pas. La région distale de la face antérieure du tibia est en général innervée par un rameau issu du nerf 4 et non par le nerf 3, comme dans les tibias méso- et métathoracique.

Les variations individuelles du plan général d'innervation signalées dans la patte mésothoracique se retrouvent dans la patte prothoracique.

## CONCLUSION

L'organogenèse sensori-nerveuse se fait progressivement au cours de la vie larvaire ; elle est caractérisée par une augmentation du nombre des récepteurs sensoriels plutôt que par une modification du plan d'ensemble. Chez la larve néonate, on peut déjà mettre en évidence un plan général des grands tronc nerveux qui sera celui de l'adulte. Les sensilles sont alors assez peu nombreuses, mais elles se reforment à chaque mue et gardent leur position relative au cours du développement post-embryonnaire. Les sensilles formées chez les larves des premiers stades du développement acquièrent une grande taille chez les nymphes, ce qui permet de les reconnaître aisément. On les retrouve également chez l'imago et ce sont les sensilles qui atteignent les plus grandes dimensions. Ceci a été confirmé par l'observation d'individus colorés peu avant la mue et montrant l'ancienne cuticule avec les anciennes sensilles entourant la nouvelle cuticule et les nouvelles sensilles. Lorsque le prolongement nerveux distal d'une ancienne sensille n'est pas encore sectionné, il passe à l'intérieur de l'orbite basale de la sensille de remplacement. Ainsi, on a pu suivre la destinée des organes sensoriels.

Toutefois, il faut remarquer que la différenciation de nouvelles sensilles au cours du développement délimite des territoires bien définis. Certains de ces territoires sont particulièrement riches en sensilles diverses (trochanter, région proximale du tibia et tarse). Corrélativement à la multiplication intense des sensilles, il se forme de nombreuses arborisa-



tions sensorielles. Les nerfs principaux deviennent très gros et il apparaît des rameaux nerveux secondaires importants dans ces régions.

Il faut aussi remarquer que l'accroissement du nombre des organes sensoriels ne se fait pas toujours au même rythme. C'est ainsi que, chez les larves des quatre premiers stades du développement, ce rythme est assez lent ; les organes sensoriels sont alors peu nombreux et peu différenciés ; les larves ressemblent à la larve néonate, mais les grandes lignes du plan d'organisation sensori-nerveuse se précisent. A partir du cinquième stade de développement, le rythme de multiplication des organes sensoriels croît rapidement, ces organes se différencient en même temps que se délimitent les territoires ; le plan d'organisation nerveuse atteint son maximum de précision. L'imago ressemble d'assez près aux nymphes.

J'ai observé des phénomènes de régression des organes sensoriels sur les pattes des pseudergates, cette régression s'observant aussi pour les ébauches oculaires et les ébauches alaires.

### *Zusammenfassung.*

Die Studie behandelt die Innervation der Beine von *Calotermes flavicollis* Fab. Es wurde festgestellt, dass die gesamte sensoriel-nervöse Anlage schon bei den Larven des ersten Entwicklungsstadiums vorhanden ist und sich nicht mehr verändert, und dass nur mit jeder stattfindenden Häutung die Anzahl der sensoriellen Organe zunimmt und begleitet ist von einer reicher werdenden Verzweigung der Sinnesnerven. Gleichzeitig entstehen sekundäre Abzweigungen der Sinnesnerven, welche von den Hauptnerven ausgehen. Die Extremitäten der Larven des vierten und hauptsächlich des fünften Stadiums weisen eine sehr starke Zunahme der Sinnesorgane auf. Diese letzteren haben dann verschiedene Grösse und stehen je nach Region des Beines mehr oder weniger dicht beisammen. Dieselben Verhältnisse finden sich auch bei den Nymphen und Imagines.

Eine zahlen- und grösssenmässige Regression der Sinnesorgane wurde bei der Entstehung der Pseudergaten festgestellt. Die Anatomie der Sinnesorgane des dritten Beinpaars ist derjenigen des mittleren Beinpaars ähnlich. Die vordere Fläche des vordersten Beinpaars ist der hinteren Fläche des mittleren Paares ähnlich und die hintere Fläche derjenigen der Vorderfläche des mittleren Beinpaars.

### *Summary.*

The author studies the developpement of the neuro-sensorial organs on the legs of *Calotermes flavicollis* Fab. He has found that the outline of the neuro-sensorial organs developing in the larvae of the first instar do not change their structure. After each molt the number of sensorial organs increases and in correlation with this the small sensorial nerves

ramify and secondary nerfs branch off the primary nerfs. On the legs of the larvae of the forth and mainly on those of the fifth instar the number of sensorial organs increases considerably. These latter are of different size and sit according to the region of the leg more or less densely together. The same is observed on the nymphs and imagines.

A regression of the number and size of the sensorial organs accompanies the development of the pseudergates.

The anatomy of the neurosensorial system of the third pair of legs is alike that of the second pair. The first pair of legs shows on the front surface the anatomy found in the hind surface of the second pair of legs and the hind surface of the first pair the one of the front surface of the second pair.

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# SUR LE NID ET LA BIOLOGIE DE *CORNITERMES CUMULANS* (KOLLAR), TERMITES BRÉSILIEN

Par Pierre-P. GRASSÉ (1)

Dans l'État de São Paulo, *Cornitermes cumulans* (Kollar) (2) est un Terme fort commun, dont les nids abondent dans les lieux herbeux et sur les emplacements d'anciennes plantations. J'ai eu l'occasion d'étudier la structure de ses édifices et de faire quelques observations sur son comportement.

Le nid de *Cornitermes cumulans* se trouve toujours dans des terres contenant une forte proportion d'argile. Il parcourt un cycle de développement qui le fait passer d'une situation entièrement hypogée à un état en grande partie épigé, tandis que sa structure subit des remaniements d'une certaine importance.

## 1<sup>er</sup> STADE.

### Nid entièrement hypogé.

Rien extérieurement ne trahit sa présence ; seule la fouille heureuse d'un terrain où les nids épigés abondent permet de le découvrir. Les nids de ce type, que nous avons eu la bonne fortune

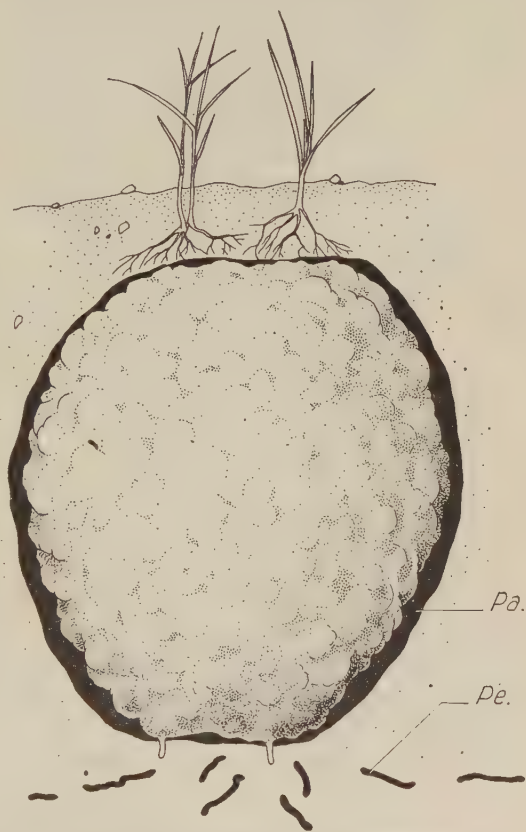


FIG. 1. — *Cornitermes cumulans*. Nid hypogé vu en place et non ouvert.

Pa, paraécie ; Pe, galeries de la péricie.

(1) Ce travail a été réalisé grâce à l'aide matérielle qu'a bien voulu m'accorder le Conseil de la Recherche scientifique du Brésil, à qui j'exprime mes vifs remerciements.

(2) Comme l'a montré EMERSON (1949 et 1952), le Terme que SILVESTRI (1903) a étudié sous le nom de *Cornitermes cumulans* ne correspond pas à l'espèce de Kollar. Notre Collègue américain en a fait une espèce particulière *Cornitermes silvestrii*. Ajoutons que le nid de *C. silvestrii* diffère beaucoup de celui de *C. cumulans*.

d'observer, étaient déjà de grande taille et prêts à saillir à l'extérieur. (fig. 1)



FIG. 2. — *Cornitermes cumulans*, nid hypogé ouvert pour montrer la structure interne. Remarquer les racines qui se développent dans la région alvéolaire du nid.

la terre sus-jacente. Ce rapport d'intimité n'existe probablement pas dans le cas de nids plus jeunes.

La paroi de l'édifice, telle que nous l'avons observée, était continue et les galeries de la périécie partaient surtout du pôle inférieur en contact avec la terre ; aucune communication n'existait sur les côtés de la muraille, alors qu'au stade suivant on en comptera plusieurs.

Ouvert, le nid montrait une structure hétérogène (fig. 2) dans laquelle on reconnaissait :

1. **Une zone externe ou muraille**, épaisse de 5 à 9 cm, creusée de galeries et de chambres grossières disposées sans ordre. Le matériau qui la compose est surtout de l'argile ; mais la surface extérieure du nid, comme les parois des chambres, sont recouvertes d'un enduit noir, fait probablement d'excréments, déposés liquides puis durcis en desséchant. Cet enduit, examiné à la loupe binoculaire, a un aspect luisant, vernissé ; il est continu. Son épaisseur est de l'ordre de

Les tout premiers stades nous manquent.

Ils affectaient une forme grossièrement ovoïde (gros bout tourné vers le haut) et mesuraient 30 cm de plus grand diamètre et 35 cm de grand axe. Leur surface était irrégulièrement mamelonnée. Entre eux et la terre environnantes intercalait un espace vide qui correspond à la *paraécie* que GRASSÉ et NOIROT (1948) ont décrite autour de divers nids souterrains de Termites africains (*Macrotermes*, *Acanthotermes*, *Sphaerotermes*, *Apicotermes*). L'espace était étroit et ne dépassait guère 1 à 2 cm d'épaisseur. Le nid reposait par son pôle inférieur (généralement le moins obtus) sur le sol ; par son pôle supérieur, il était en contact avec



FIG. 3. — *Cornitermes cumulans*, masse noirâtre faite en grande partie de matériaux stercoraux et adhérent à la paroi par un pédoncule.  $\times 2$ .



0,3 mm à 0,5 mm. La matière terreuse des parois (argile rougeâtre) contient des trainées, des plaques de matière noire, identique au revêtement superficiel ; ce qui indique que l'Insecte, en construisant, peut mélanger aux excréments les matériaux terreux prélevés à l'extérieur.

Certaines chambres de la zone externe contiennent des masses noirâtres qui, pour la plupart, adhèrent aux parois (fig. 3). Vues à la loupe binoculaire, ces corps apparaissent comme étant faits d'une pâte noirâtre, stercorale, dans laquelle sont pris les débris végétaux, abondants au point de se toucher.

2. *Une zone centrale ou noyau.* — Elle est presque sphérique (16 cm sur 17 à 18 cm) et faite de cloisons superposées, à orientation assez désordonnée, et à peu près horizontales dans la région inférieure. Souvent irrégulière, leur épaisseur varie de 0,3 mm à 1 mm ; elles présentent çà et là des renforcements épais de 3 à 4 mm.

La matière qui constitue les cloisons du noyau est d'un aspect bitumeux, noir mat ; vue à la loupe, elle rappelle celle de l'enduit superficiel et paraît faite de la superposition de couches liquides, très vraisemblablement stercorales, desséchées.

Les racines des fortes Graminées qui poussent au-dessus du nid traversent celle-ci de part en part. Dans la zone centrale, elles se ramifient en un chevelu si dru qu'on peut se demander si les Termites (ou les conditions qui règnent dans la termitière) ne stimulent pas leur poussée et leur ramification. Ici comme je l'ai observé, très souvent, dans maintes termitières africaines, les ouvriers respectent les racines vivantes qui pénètrent dans leur nid et, à leur sortie de celui-ci, ils les entourent d'un épais manchon noir, fait du même matériau que la muraille (fig. 4).

La paraécie n'est pas un lieu d'habitation ; elle est pratiquement séparée du nid et, d'ordinaire, ne contient pas d'ouvriers. Elle a le même caractère dans les nids de *Macrotermitinæ* et d'*Apicotermittinæ*.

La paraécie dans les nids des *Macrotermitinæ*, des *Apicotermittinæ* et des *Nasutitermitinæ* (*Cornitermes*) n'a probablement pas la même valeur chez tous. Nous ne connaissons son origine que chez certains *Macrotermitinæ*, où elle représente l'espace qui sépare la cellule royale primitive de la terre qui l'entoure. Dans le cas de nids polycaliques : *Acanthotermes*, *Synacanthotermes*, *Apicotermes*, elle est construite d'emblée, que la calie contienne ou non une cellule royale. Sur l'origine de la paraécie des *Cornitermes*, nous ne savons rien.



FIG. 4. — Racine de Graminée sortant du nid et recouverte, à son passage à travers la paraécie, d'un manchon de matériaux noirâtres, vraisemblablement de nature stercorale.

**2<sup>e</sup> STADE. Nid partiellement épigé, recouvert d'un dôme de terre.**

Le nid souterrain s'accroît surtout par sa partie supérieure et semble refouler vers le haut la terre qui le surmonte. Dans la réalité, le processus n'a pas cette simplicité. En effet, l'accroissement en hauteur du nid s'accompagne du remaniement de la terre située au-dessus de l'habitation et d'un apport important de matériaux dans cette zone.

Examinons un nid particulier.

De l'extérieur, il apparaît comme une masse de terre rouge formant deux dômes inégaux et largement fusionnés à leurs bases, masse de contour oblong, mesurant 50 cm de grand axe, 40 cm de petit axe et 16 cm de haut.

La veille de l'ouverture de ce nid (25 avril), il avait légèrement plu et, au moment de la fouille, la terre conservait une certaine humidité ; pendant



FIG. 5. — *Cornitermes cumulans*, nid devenant partiellement épigé.

*Pa*, paraécie ; *Pe*, périécie ; *Tb*, tube traversant la paraécie et conduisant dans les galeries de la périécie.

la nuit, des ouvriers avaient construit une forte bosse flanquant le plus petit des deux dômes. Au moment de l'ouverture, les ouvriers procédaient au renforcement de l'ébauche alvéolaire de cette bosse, par des apports de terre argileuse.

La termitière se compose de deux parties distinctes bien que continues : le *nid proprement dit*, que délimite la paraécie, et le *dôme terreux*, qui le surmonte.

Le nid proprement dit, à peu près sphérique, mais à pôle supérieur tronqué, est limité par une paroi noirâtre et mamelonnée (fig. 5) ; sa hauteur est de 30 cm. Comme au stade précédent, de nombreuses racines de Graminées le traversent de part en part, et, à leur sortie, sont entourées épais manchon noirâtre déjà signalé.

La paraécie est d'une grande netteté ; son épaisseur, selon les endroits, varie de 1 à 5 cm. Elle n'est pas maçonnée ; les *Cornitermes* se contentent, pour la faire, d'enlever la terre qui se trouve au contact du nid.

Les communications latérales du nid proprement dit avec la périécie ne sont pas nombreuses. La paroi du nid envoie vers l'extérieur des saillies creuses qui traversent la paraécie et aboutissent en plein dans la terre environnante. Ce sont des tubes creux (fig. 5, *Tb*) de forme grossièrement cylindrique ; nous en avons compté jusqu'à une douzaine (dans d'autres nids, il y en avait moins, dans d'autres plus).

Le nid, à peu près exactement à son pôle inférieur, se continue vers le bas par un tube construit comme les tubes latéraux et qui pénètre dans la terre sous-jacente, un peu obliquement. La lumière du tube a pu être sondée sur une profondeur de 15 cm et va certainement beaucoup plus bas. Le tube sur tout ce trajet est délimité par une paroi maçonnée, et n'est pas qu'une galerie creusée à même le sol. Ce tube « polaire » donne l'impression d'être la principale voie de communication du nid avec la périécie.

Le pôle supérieur du nid proprement dit, fortement tronqué, se continue insensiblement avec le dôme épigé qui le surmonte. Il existe en effet une zone de transition entre les deux, zone où le *Cornitermes* a effectué une construction d'une nature particulière.

Cette zone se compose d'alvéoles irréguliers maçonnés directement sur la muraille, noire et compacte, au pôle tronqué du nid. Leurs parois, plus minces que celles des cellules du nid, sont faites de terre argileuse, en boulettes de taille inégale et de forme variée.

Les alvéoles communiquent avec le nid par des ouvertures percées dans la muraille, circulaires, et mesurant de 2 à 3 mm de diamètre. Alors que la muraille se compose de matériaux compacts et résistants, la zone alvéolaire de transition est faite de matériaux terreux, faiblement agglomérés, qui perdent leur cohésion en séchant et deviennent friables.

La zone de transition fait passer insensiblement du nid au dôme épigé où la terre est très grossièrement maçonnée.

### 3<sup>e</sup> STADE. *Nid en grande partie épigé et sans dôme de terre le recouvrant.*

On peut considérer ce stade comme correspondant à l'état terminal du nid qui, bien que sous cette forme, continue à s'accroître. L'étude

comparative de divers nids nous a appris que le passage du deuxième au troisième stade se fait progressivement, le dôme alvéolaire étant « absorbé » par la paroi supérieure du nid proprement dit. A la terre argileuse peu cohérente se substitue un matériau plus consistant ; le remaniement de la termitière paraît être très important chez *Cornitermes cumulans*.

Prenons à titre d'exemple un nid haut de 1,60 m et de 0,95 m de diamètre à sa base ; ce nid se trouve en partie accolé à un talus.

Il est entouré d'une muraille épaisse de 9 à 12 cm, faite de matériaux compacts et résistants ; elle est parcourue par un réseau com-



FIG. 6. — *Cornitermes cumulans*. Grand nid épigé, vu en coupe longitudinale.

*Pa*, paraécie ; *Zf*, zone feuilletée ; hauteur du nid 1,60 m.

pliqué de galeries sinueuses et larges, qui toutes sont tapissées d'un enduit noirâtre. La continuité, entre les parties épigée et hypogée, est parfaite (fig. 6).

Dans la partie supérieure du nid (à peu près le tiers de la hauteur totale), la muraille se continue insensiblement avec les parties profondes, mais plus on s'approche de la région axiale, plus les parois des galeries perdent de leur épaisseur, et les alvéoles sont remplacés par des chambres très plates, irrégulières, à peu près horizontales. L'aspect global de cette région est feuilleté.



La paraécie subsiste très nette dans la partie hypogée du nid et monte bien au-dessus de la surface du sol (1). Elle fait penser à celle qui s'observe dans les calies des *Acanthotermes* africains.

La partie centrale du nid, isolée de la muraille par la paraécie, a une structure feuilletée très caractéristique (fig. 6, *zf*). Les matériaux en sont plus fins que ceux de la muraille.

Les communications du nid avec la périécie se font directement par des galeries qui serpentent dans la base de la muraille. Les ouvriers ont la possibilité de passer de l'endoécie dans la périécie sans avoir à traverser la paraécie.

Les matériaux que *Cornitermes cumulans* utilise pour construire sont la terre argileuse et les excréments. Les murailles sont composées surtout de terre, alors que les parties les plus profondes s'enrichissent en matières excrémentielles ; en outre, les excréments servent à confectionner les enduits dont nous avons parlé à plusieurs reprises.

Quel que soit le stade auquel appartienne la termitière, la population, y compris le couvain et le couple royal, habite le noyau, la région centrale du nid. Le couple royal, même dans les plus grandes termitières ouvertes par nous, ne dispose pas d'une cellule particulière. La reine, malgré sa physogastrie, se meut avec passablement d'aisance et conserve la faculté de passer d'une chambre dans une autre.

La population des grands nids, pendant la fouille, abandonne la région centrale du nid et s'entasse dans la muraille.

En avril-mai, aux environs de São Paulo et de Campinas, les nids de *Cornitermes cumulans* contenaient de nombreuses nymphes (aux deux derniers stades), à abdomen énorme, gonflé par un tissu adipeux surabondant, tandis que les ovaires demeuraient petits et contenaient seulement de minuscules ovocytes. A cette époque de l'année, la reine ne pond, nous a-t-il semblé, que fort peu. Les œufs en effet dans les termitières explorées par nous étaient plutôt rares.

### Summary.

*Cornitermes cumulans*, found in the state of São Paulo, first builds a subterranean nest. Accompanied by important structural changes the Termites transform it later on into a mound nest above ground. Nest building shows the following phases:

(1) DA COSTA LIMA (1939) représente (page 308, fig. 150) un grand nid de *Cornitermes* sp. qui pourrait bien appartenir à l'espèce *cumulans* (KOLLAR.). Une paraécie, très nette, y sépare la muraille massive et traversée de galeries de la zone centrale alvéolaire et feuilletée. Le caractère le plus intéressant de ce nid, en grande partie épigé, est la continuité de la muraille avec le sommet de la zone alvéolo-feuilletée ; continuité qui place le nid à un stade intermédiaire entre nos stades 2 et 3. La paraécie semble se prolonger dans un épais cylindre maçonné qui s'appuie contre une grosse branche ou l'entoure.

*First phase*

*The subterranean nest.* The very first part of this phase could not be observed. The nests found and studied by the author are egg shaped and have already a diameter of about 30 cm. The surface is warty. Between the nest and the surrounding soil there is a cavity about 2 cm. thick. The nest stands with its smaller pole on the soil. The galleries leaving the nest are all at the basis where the nest lies in contact with the soil. The nest itself consists of two parts.

1. *Nestwall*: it is 5-9 cm. thick and contains irregular galleries and chambers. The building material consists mainly of clay. But galleries and chambers as well as the outer surface of the nest are covered with a 0,5 mm thick layer of a black varnish-like mass. Even some of the outer chambers are filled with this material which under the microscope reveals to be a mixture of stercoral excrement-mass and remains of plant material.

2. *Nest center*: The inside of the nest has an almost spherical form and consists of a great number of irregular cells, the walls of which are about 0,5 to 1 mm thick. In the lower part of the nest these cells are generally horizontal. The wall material seems to be of the same matter as the wall cover of the outer part. The cavity that surrounds the nest is not inhabited by the Termites and has the same character as that found in the nests of *Macro* and *Apicotermes*.

*Second phase*

*Nest only partly subterranean with an earth covered mound above.* The subterranean nest grows at its upper pole and shows two different zones. The subterranean nest of the described form has at this phase also lateral tube shaped exits which pierce the cavity surrounding the nest and open into the soil. The big tubes however at the lower pole continue to form the main exits of the nest. The upper pole of the nest is partly cut off and flattens out gradually over the cupole of earth above the nest. The transitional zone between nest and earth-mound contains a lot of alveoli of irregular form, the thin walls of which are made of clay. This zone lies directly on the upper part of the nestwall of the first phase. Small holes in the compact nestwall lead into the alveolar zone.

*Third phase*

*Superterrestrial nest, not covered by earth.* Now the ever growing nest has its final aspect. The alveolar zone above the subterranean nest has slowly been included into the nest. The solid nestwall has been pushed up

above ground and the wall of the alveoli replaced by a more solid type of material. The entire upper structure of the nest, which can be 1,60 m high with a basic diameter of 0,95 m, is now surrounded by a strong wall, becoming thicker towards the top of the termite hill, in which we find irregular galleries and chambers with their characteristic tapestry. The subterranean part and the hill form one solid nest. In the uppermost part where the wall gradually thickens to form the top, the inside of the nest is made of irregular flat cells with foliated walls. The cavity between the subterranean part of the nest and the soil still exists. The central part of the nest has the characteristic flat foliated cells. The building-material consists mainly of excrements.

The royal couple has no specific cell. In spite of her physogastric body the queen can move about and wander from one chamber to the other. In April and May the nests around São Paulo contain a lot of nymphs of the fore-last and last instars. During this season the queen seems to lay few or no eggs at all, as few eggs are found in the nest during this period.

### *Zusammenfassung.*

*Cornitermes cumulans* findet sich im Staate São Paulo sehr zahlreich. Das Nest entwickelt sich aus einem unterirdischen Anfangsstadium zu einem grösstenteils überirdischen Bau und bedingt bedeutende Struktur-Veränderungen.

#### *1. Stadium*

*Unterirdisches Nest.* Die ersten Anfangsstadien der Nester konnten nicht beobachtet werden. Die vom Autor studierten und zufällig gefundenen sind schon recht gross und haben Eiform. Ihr grösster Durchmesser beträgt etwa 30 cm. Die Oberfläche ist unregelmässig warzig. Zwischen Nest und Erde befindet sich ein Hohlraum, welcher bis zu 2 cm Dicke hat. Das Nest ruht mit seinem spitzeren Pol auf der Erde. Die aus dem Nest führenden Galerien befinden sich an der Nestbasis. Das geöffnete Nest zeigt eine heterogene Struktur, nämlich :

1. *Die Nestwand* ist 5-9 cm dick und von Gängen und Kammern, die unregelmässig angelegt sind, durchzogen. Das Baumaterial besteht zur Hauptsache aus Lehm. Die Gänge und Kammern wie auch die äussere Oberfläche des Nestes sind mit einer lackähnlichen glänzenden Masse von etwa 0,5 mm Dicke vollständig überzogen. Einige Kammern der Mauerzone sind mit ähnlichem Material gefüllt, das sich unter der Lupe betrachtet als ein Gemisch von sterkoraler Exkrementmasse und vegetabilen Produkten erweist.

2. *Der beinahe sphärische Nestkern* besteht aus einer grossen Zahl von unregelmässigen Zellen, deren Zwischenwände etwa 0,5 bis 1 mm Dicke haben. Sie liegen im unteren Teil meist horizontal. Das Material der

Zwischenwände scheint desselben Ursprungs zu sein wie der Wandüberzug der äusseren Gänge.

Der das Nest umgebende Luftraum ist von den Termiten nicht bewohnt und hat denselben Charakter wie bei den Macro- und Apico-Termiten.

## 2. Stadium

*Teilweise überirdisches Nest, von Erdkuppel bedeckt.* Das unterirdische Nest wächst am oberen Pol und weist zwei gut unterscheidbare Teile auf. Das eigentliche unterirdische Nest von der beschriebenen Form hat im jetzigen Stadium auch laterale Ausgänge, welche als Röhren den das Nest umgebenden Hohlraum durchstossen und in die Erde münden. Die Hauptausgänge befinden sich jedoch an der Basis, wo eine Röhre in die Tiefe stösst. Der obere Pol des Nestes ist abgeschnitten und geht langsam in die Erdkuppel über, welche über dem Nest errichtet wird. Die Übergangszone zwischen Nest und Erdkuppel enthält zahlreiche Alveolen unregelmässiger Form, deren dünne Wände aus Lehm errichtet sind. Diese Zone liegt direkt auf dem obersten Teil der Wand des eigentlichen Nestes. Kleine Öffnungen führen aus der kompakten Nestwand zu den Alveolen in der Erdkuppel.

## 3. Stadium

*Überirdisches Nest, nicht von Erdhügel bedeckt.* In diesem Stadium hat das immer noch wachsende Nest seinen definitiven Aspekt erreicht. Die alveoläre Zone des Erdhügels über dem ursprünglichen Nest wurde allmählich ins Nest einbezogen, die solide Nestwand nach oben geführt und die Wände der Alveolen durch solideres Material ersetzt. Der ganze Oberbau eines Nestes von etwa 1,60 m Höhe und 0,95 m Basisdurchmesser ist jetzt von einer soliden Mauer umgeben, die von schwarz austapezierten Gängen durchzogen ist. Ober- und unterirdischer Bau gehen kontinuierlich ineinander über. Im obersten Teil des Nestes (ca. 1/3 der Gesamthöhe) wird die Mauer dicker und geht nur ganz allmählich in den Innenteil über, der hier platte, unregelmässige Zellen besitzt mit Wänden wie Blätterteig. Der Hohlraum zwischen Erde und unterirdischem Teil besteht immer noch und reicht jetzt sogar über das Bodenniveau hinaus. Der Zentralteil des Nestes hat eine charakteristische blätterige Struktur. Das Baumaterial besteht hier zur Hauptsache aus Exkrementen.

Das Königspaar hat keine spezielle Zelle. Trotz ihrer Physogastrie kann sich die Königin bewegen und von einem Raum in den anderen gelangen. Im April und Mai enthalten die Nester von São Paulo zahlreiche Nymphen der zwei letzten Stadien. In dieser Jahreszeit scheint die Königin nicht oder kaum Eier zu legen, denn die Eier in den untersuchten Nestern waren selten.



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(1) Dans le catalogue de SNYDER (1949), EMERSON a établi la véritable synonymie de *Cornitermes cumulans* (T. E. SNYDER). — (Catalog of the Termites [Isoptera] of the world. *Smith. Miscell. Collect.*, vol. 112, page 262, 1949).

## EXPLICATIONS DES PLANCHES

### *CORNITERMES CUMULANS*

#### PLANCHE I.

Nid partiellement épigé, montrant nettement la zone alvéolaire de transition entre le nid proprement dit et le dôme de terre. Sur la gauche, un canal latéral de communication traversant la paraécie. Çà et là, quelques orifices s'observent à la surface du nid.

#### PLANCHE II.

Coupe verticale du même nid extrait du sol, montrant la zone périphérique, ou muraille alvéolaire, et la zone centrale plus ou moins feuilletée.

#### PLANCHE III.

Le dôme et la zone de transition vus au-dessus du nid retiré du sol.

#### PLANCHE IV.

1, 2, 3 et 4, étapes de la fouille d'un nid partiellement épigé. En clair une partie, fraîchement construite. La paraécie, après la fouille, apparaît comme une grande poche subsphérique; — 5, grand nid schématisé dans la figure 6 de ce texte; la paraécie se voit nettement à droite et en bas.



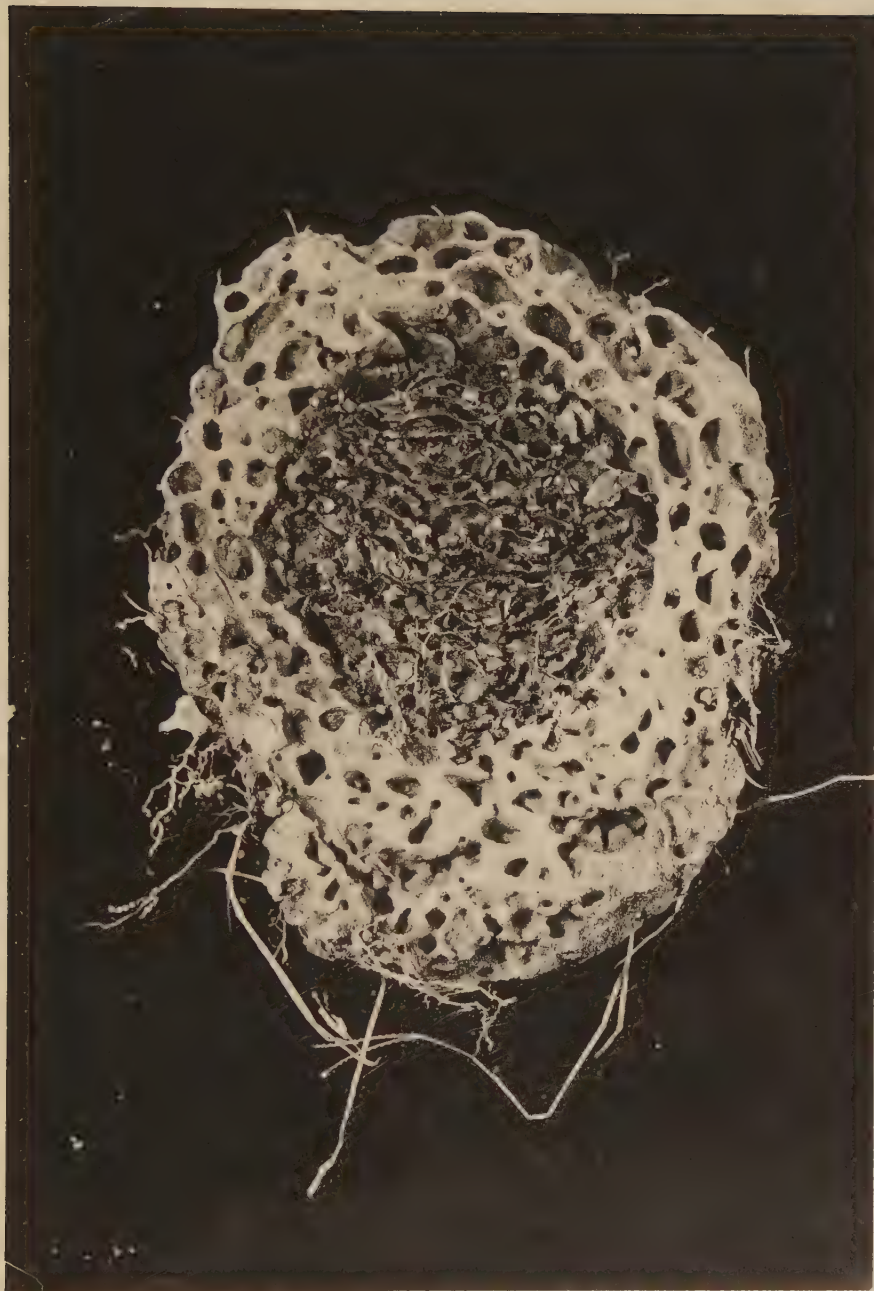
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*Cornitermes cumularis*







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Phototype Duval.

*Cornitermes cumularis*





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Phototypie Duval

***Cornitermes cumulans***

Masson et C<sup>ie</sup>







1



2



3



4



5

*Cornitermes cumulans*



# REPRODUCTION, NEST ORIENTATION AND POPULATION STRUCTURE OF AN AGGREGATION OF MOUND NESTS OF *FORMICA ULKEI* EMERY (« FORMICIDAE »)

by

Gerald SCHERBA

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## Introduction.

The conspicuous ant mounds characteristic of a number of species of *Formica* and other genera are an arresting sight, and in this paper some of the features of the nest structure and life history of one mound builder will be described. These observations were made in the course of field studies between 1950 and 1955 at an aggregation of mound nests of *Formica ulkei* Emery near Lemont, Illinois, in Cook County, about 30 miles southwest of Chicago.

The nests are located in a mixed oak-hickory forest dissected by sloping meadows on an upland portion of the Valparaiso moraine. The soil is glacial clay covered by a humus layer of varying thickness.

*Formica ulkei* is one of three mound-building members constituting the *exsecta* group of the subgenus *Formica* along with *F. exsectoides* Forel and *F. opaciventris* Emery. According to CREIGHTON (1950) *opaciventris* and *exsectoides* are more closely related to each other than to *ulkei*. GREGG (1952) suggests that *opaciventris* may in fact be a Western subspecies of *exsectoides* as WHEELER (1913) originally proposed. Within the group the habits of *exsectoides* are best known, due principally to a series of detailed observations by ANDREWS (1925, 1926, 1927, 1932). With an increasing knowledge of *ulkei* and *opaciventris* the *exsecta* group would appear to be ideal subjects for the comparative study of behavior.

The geographical distribution of *ulkei* is to the north and west of *exsectoides* and to the east of *opaciventris*. *F. ulkei* ranges east to Nova Scotia, Ontario, west to Manitoba, and North Dakota and south to Ohio, northern Indiana and Iowa. In the Chicago area, the ranges of *exsectoides* and *ulkei* overlap, but there is no indication of hybridization. The story of the initial discovery of *ulkei* in the type locality, Hill City, S.D., by TITUS ULKE in 1890 is an interesting one, and has recently been recounted by SMITH (1952).

Within the Chicago area, GREGG (1944) reports *ulkei* from six widely scattered localities; Palos Park, Ill., Palatine, Ill., Waukegan, Ill., Volo, Ill., Dune Acres, Ind., Smith, Ind., and Lakeside, Mich. However it is only in the first two localities that *ulkei* occurs in groups of nests, and at the Palos Park locality there are over 250 nests within a 50 acre area of forest and meadow. Despite this sizeable number of nests, *ulkei* has not been found in the adjacent similar forests which extend for miles to the east, west and north constituting the Cook County Forest Preserves. This distribution is certainly anomalous.

The particular aggregation of mound nests upon which the observations reported here are based has been subjected to a surprising amount of inspection by various investigators over the past 30 years. HOLMQUIST's (1926, 1928, 1928 a) interest in

arthropod hibernation led him to investigate the winter conditions in *Formica ulkei* mounds and then to describe the life history along with some of the myrmecophiles found within these mounds. Later T. PARK (1929) and O. PARK (1929, 1935) added to the list of myrmecophiles and described the nature of the relationships between some of these insects and *ulkei*. The population size of this aggregation of mound nests and the ecological distribution with respect to forest, margin and clearings was determined by DREYER and T. PARK (1932) who found strong coincidence between the forest margin and clearings and the location of *ulkei* mounds. In 1941 DREYER returned to recensus this same population and record the changes that had occurred in this interval (DREYER, 1942). SCHERBA (in press) compared the temperature and moisture content of a series of mound nests with that of the adjacent soil and interpreted these differences as indicating the operation of social homeostatic mechanisms.

Certain physiological studies have also been conducted. HOLMQUIST (1928 a) measured the Respiratory Quotient and water content of both hibernating and active workers while DREYER (1932) determined that the Respiratory Quotient of *ulkei* has a seasonal rhythm, decreasing at low temperatures and varying with diet. TALBOT (1934) tested the tolerance of *ulkei* and five other *Formica* species to high temperatures and low humidities.

## REPRODUCTION

**Seasonal cycle of activity.** — The field observations of HOLMQUIST (1928, 1928 a) and the author in 1950, 1951, 1953 and 1954 indicate that there is a regular and predictable sequence of events occurring within the mound nests. These events will vary from year to year and from nest to nest apparently dependent upon environmental factors, especially temperature. Microclimate is particularly important in this respect, and the mound that is shaded or has only a northern exposure to the sun lags in activities such as the development of the brood and the initiation of activity in the Spring.

TABLE I. — SEASONAL CYCLE OF EVENTS IN NESTS OF *Formica ulkei* EMERY.

SEASON	EVENT
Mid March .....	Surface activity begins.
April .....	Nest construction begins.
	Active defense of nest begins.
	Foraging activity begins.
Late April-May .....	Egg laying.
May-Mid August .....	Development of worker larvae.
Early June-Mid September .....	Development of worker pupae.
Mid July-Mid October .....	Emergence of workers.
Mid April-Mid June .....	Founding of new nests by budding.
May-June .....	Development of sexual larvae.
Early June-Early July .....	Development of sexual pupae.
Mid June-Early July .....	Emergence of males.
Late June-Early July .....	Emergence of females, after males.
Early-Mid July .....	Mating flight.
Late September-October .....	Activity declines.
Late October .....	Activity slight.
Late October-Early November .....	Activity ceases.



Activity above ground begins about the middle of March and there is a gradual commencement of activities such as foraging, nest building and defense of the nest. Egg laying begins in April and the subsequent cycle of brood development is summarized in Table I. Coinciding with the appearance of eggs in the colony, certain mound nests produce bud nests a short distance from the parental nest. Later in the season, in early July, the mating flight occurs. Beginning at about the time of the mating flight, large batches of empty pupal cases can be found on the mound perimeter indicating the emergence of workers. Workers will continue to emerge throughout the summer and by October all of the brood has emerged and the colony enters hibernation with only workers and queens.

**Formation of bud nests.** — Between April, 1953, and October, 1954, 63 mound nests were formed by budding from parental nests. This process, which WHEELER (1910) termed *hesmosis*, takes place in late April, May and early June and has never been observed to occur at any other time of the year.

The factors which act to induce budding are obscure, although in one case, nest 52, the entire colony migrated into a clearing less than two feet from their former nest which was being heavily shaded by overhanging grape vines. In another instance, nest 112, a vigorous colony appeared to be heavily shaded by Hawthorn trees *Crataegus* sp., and it produced four bud nests all in the direction of less shade.

Choice of a site for a new nest appears influenced by light intensity and the nature of the substrate. Most of the bud nests from parental nests situated at the forest margin were located in the direction of the clearing rather than toward the forest or alongside the parental nest. Soil that has been mined or at least cleared of the plant cover is favored as a site. Thirteen of the bud nests were located on inactive nests of *F. ulkei* or *F. fusca*. One was founded at the site of a crayfish midden formed earlier in the year, and several nests were founded at the base of grass clumps. In this latter case, the tall grass stems are utilized as posts and buttresses for the construction of the mound. Distance of bud from a parental nest varies from a few to 30 feet.

Size of the incipient nest appears to vary with that of its population. Large buds with several hundred workers have been found with a basal diameter greater than 18 inches within a few weeks after founding. Some of the recently founded buds contain no brood. Workers have been observed transporting worker larvae from a parental to a bud nest. It is not known whether the bud nests contain a queen shortly after founding or whether the nest queen arrives after the mating flight.

**Mating flight.** — The flight of winged sexuals from nests in the colony was observed on July 2, 7, 8, 9, 1953, and on July 8, 9, 1954, during the early morning hours.

In the days preceding the mating flight, first the males and then the females emerge from their pupal cases and can be seen walking over the surface of the nests. The males especially move as if they are trying to leave the nest while the workers cling with their mandibles to the legs and antennae of these males on the nest surface and give the appearance of forcibly detaining them.

The departure of the winged sexuals from the mound occurs during the early morning hours with the males flying off earlier than the females. Typically both males and females are released from "mature" mounds, although the relative proportions are unknown. Before leaving the mound surface, the sexuals fan their wings repeatedly, then often climb to the top of a nearby grass stem, and, when they depart, usually fly in the direction away from the forest and toward clearings and increased light intensities. At individual nests the flight departures span a two hour period, as at nest 36 on July 8, 1954, between 6.30 a.m. and 8.30 A.M. C.S.T.

Mating has not been observed. It presumably takes place outside the nest, either in the air or on the higher branches of trees.

Following the flight, the queens return to the ground where they are seen moving along the surface. A number of queens somehow find their way to the surface of mound nests where they are seized by workers who pinion them by holding legs and antennae outstretched. While the queen is held in this position, a worker shears the wings at their axis with the body using its mandibles, and the queen is dragged within the nest. When queens pinioned by workers of one nest were freed of workers and transferred to the surface of another nest, they were again pinioned and dragged within the nest. Since queens excavated weeks after the mating flight still had one or two shredded wings attached to the thorax, the removal of wings by the workers may be a variable pattern of behavior.

The return of mated queens to established nests of the same species has been called *secondary pleometrosis* by WHEELER (1910) and it is evidently a portion of the reproductive pattern in *Formica ulkei*. However WHEELER also suggested that, since *Formica exsectoides* has been shown to be a temporary social parasite of *Formica fusca*, then *F. ulkei* was doubtless similar in this respect. CREIGHTON (1934) verified WHEELER's assumption when he found a nest of *F. fusca* workers with a queen of *F. ulkei* in Hill City, S.D. Nevertheless we have not been able to repeat CREIGHTON's observation despite the fact that there are numerous nests of *F. fusca* within the study area. Evidently *F. ulkei* queens can and do act as temporary social parasites of *F. fusca*, but the rate at which they do so successfully is probably quite low. If so, then this would account for the anomalous distribution of *F. ulkei* in the Chicago area where a large aggregate of mound nests occurs due to budding, maintained by secondary pleometrosis; and widely scattered single nests also occur, miles apart, because of occasionally successful attempts at temporary social parasitism of the common and widespread *F. fusca*.

## ORIENTATION OF THE MOUND NEST

At the study area, the nests of *Formica ulkei* are asymmetrical with a long slope oriented toward the Southwest, the direction of greatest solar intensity in the Chicago area. How the mounds become oriented toward



FIG. 1. — Mound nest of *Formica Ulkei*. A piece of paper denotes the long slope oriented in the Southwest direction.



FIG. 2. — Cross section of mound nest showing thick crustal cap enclosing heterogeneous nest material. Circular and horizontal galleries extend into the soil to a depth of 5 to 6 feet.



greatest solar intensity is not known. Two possibilities exist: either the mounds are oriented toward the Southwest according to some "compass response", or else the warmer temperatures which exist on Southwest slopes, in contrast to other slopes, facilitate nest building over a longer period of time and at a faster rate.

Since, according to the second hypothesis, the direction of the long slope ought to change if the direction of greatest solar intensity is changed, we have measured the relationship between the direction from which the nest is shaded and the direction in which the long slope is oriented. In making this survey, all the mound nests which had a definite, easily discernible long slope were measured with a compass to the nearest octant. For example, on an individual nest, the shade might encompass the NW, N, NE and E directions, the long slope the SE, S, and SW

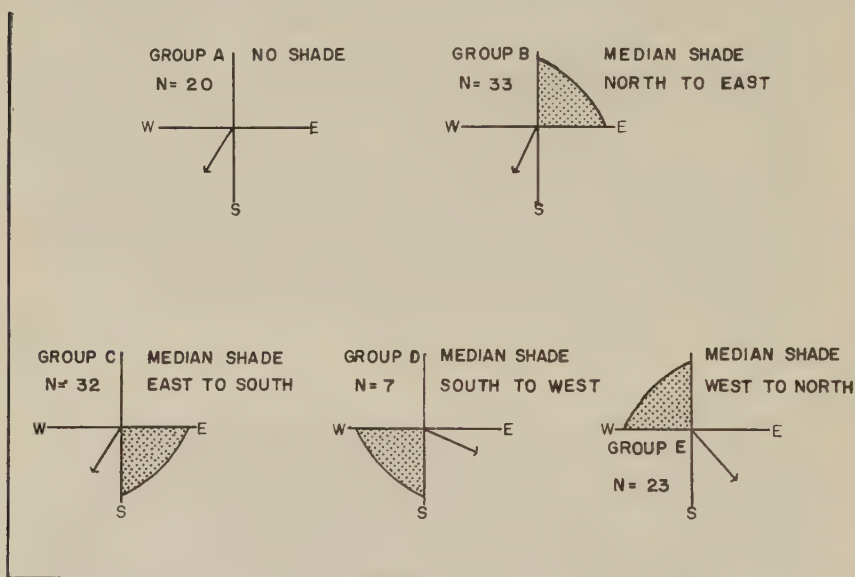


FIG. 3. — Relation of natural shade direction (stippled area) to direction in which the long slope is oriented (indicated by arrow). Alteration of direction of shading is accompanied by alteration in the orientation of the long slope. See text.

directions. As a basis for comparison, only the median direction of shade and the median direction of the long slope are considered. The compass octants were numbered clockwise from one to eight with N = 1, NE = 2, and so forth. The nests were then lumped into five groups according to the median direction of the nest shade and the mean, and Standard Error of the median direction of the long slope was calculated for each group.

Results are tabulated below and represented as figure 3. Unshaded nests have the long slope oriented in a Southwest direction, as do nests whose median direction of shade lies to the north, northeast, east, south-



east or south. When the median shade direction falls in the south to west quadrant, however, the median of the long slope is oriented just south of east. When the median shade direction is in the west to north quadrant, the median slope direction changes to southeast. Although none of the mean median slope values fall in the two northern quadrants, eight nests in groups C, D, and E do have median slope directions in the upper quadrants.

We conclude that alteration of direction of greatest solar intensity

TABLE II. — RELATION OF DIRECTION OF LONG NEST SLOPE TO DIRECTION OF SHADE.

GROUP	RANGE OF MEDIAN SHADE DIRECTION	MEAN MEDIAN SHADE DIRECTION	No. OF NESTS	MEAN MEDIAN LONG SLOPE DIRECTION ± S.E.	STANDARD DEVIATION
A	No shade	—	20	5.53 ± 0.10	0.44
B	N. to E.	1.63	33	5.42 ± 0.09	0.53
C	E. to S.	3.53	32	5.73 ± 0.25	1.44
D	S. to W.	6.26	7	3.29 ± 0.29	0.77
E	W. to N.	7.86	23	3.89 ± 0.20	0.94

is accompanied by corresponding alteration in the orientation of the long slope. The second hypothesis appears to be the more attractive of the two.

### THE POPULATION (1)

The number of mound nests, their size in basal diameter, and their distribution with respect to forest, forest margin and clearings has been determined in 1931 by DREYER and PARK, in 1941 by DREYER and in 1953 and 1954 by the author.

TABLE III. — CENSUS OF ACTIVE NESTS OF *Formica ulkei* MOUNDS CLASSIFIED AS TO SIZE (2).

	1931		1941		Mar.-Apr. 1953		Oct.-Nov. 1953		April 1954		Sept.-Oct. 1954	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Small...	137	32.7	80	28.7	25	9.9	38	14.4	30	12.0	32	11.8
Medium.	130	31.0	100	35.8	103	40.6	102	38.8	92	36.8	113	41.6
Large...	152	36.3	99	35.5	125	49.5	123	46.8	128	51.2	127	46.6
Total .	419	100.0	279	100.0	253	100.0	263	100.0	250	100.0	272	100.0

(1) The author is grateful to Prof. EARL RICH, *University of Miami*, for his advice concerning the treatment of data in this portion of the paper.

(2) Small = basal diameter < 18 inches; Medium = 18—36 inches; Large = > 36 inches.

In each survey the method of census has been to map the study area and plot the location of each nest on the map. In 1953 and 1954, numbered stakes were driven next to each nest. Since, in general, larger nests are older nests, data from such censuses provide information on both the population size and age structure as they have changed over a period of 23 years.

Examination of Table III and figure 4 indicate that after an initial decline in population size from 419 in 1931 to 279 in 1941, the number

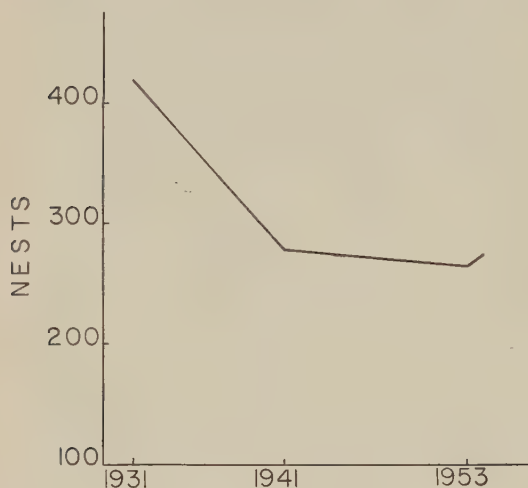


FIG. 4. — Change in number of active mounds over a 23 year period of census. Census dates were 1931, 1941, 1953, 1954.

of active mounds has remained approximately at the 1941 level. However, the relative porportion of different sized mounds has changed steadily toward an increase in the proportion of medium and large sized mounds, and a decrease in the porportion of small mounds. To the extent that this size classification reflects age distribution, there is a definite trend toward an increase in the proportion of older mounds and a decrease in the proportion of younger mounds (figure 5).

The ecological distribution with respect to forest, forest margin and clearing has remained essentially the same during the period of census.

**Mortality.** — Of the original 419 active nests present in 1931, there were 60 % surviving in 1941. If we express this as the negative rate of increase of population using the formula

$$(1 + r) = \sqrt[t]{\frac{P_0}{P_t}},$$

where  $r$  = annual rate of increase,  $t$  = interval of time in years,  $P_0$  = population size at time zero, and  $P_t$  = population at time  $t$ , we find a negative rate of increase of 5 % per year between 1931 and 1941. Of the 253 active nests present in April, 1953, 232 were surviving in April 1954, a mortality rate of 8.3 %; and of the 263 nests present in October, 1953, 228 were surviving in October, 1954, a mortality rate of 9.5 %. See Table IV.

Thus, for this population during the period of census, the overall mortality rate is between 5 % and 10 % per year. However, this mortality

is not equally distributed throughout the population but is greatest among smaller, presumably younger, nests and least among larger, presumably

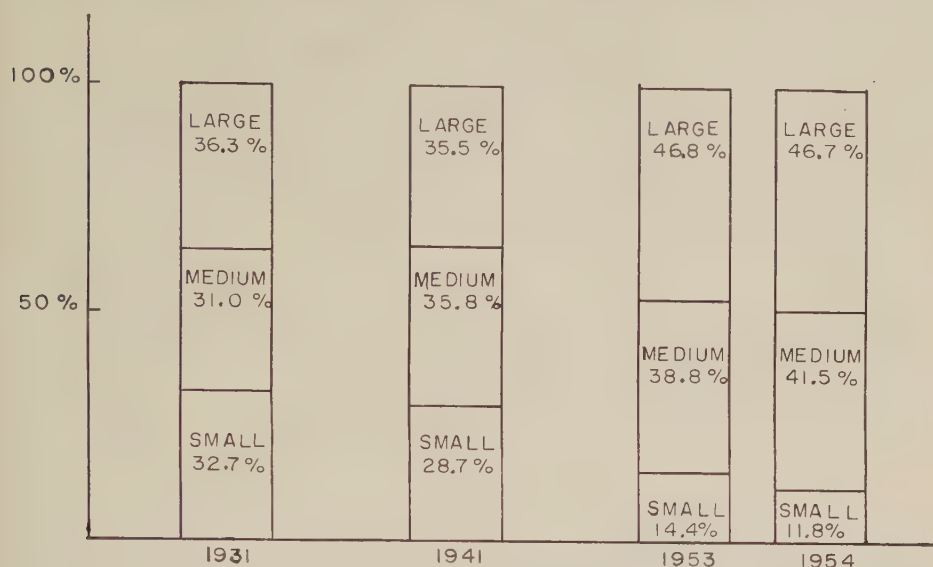


FIG. 5. — Change in percentage composition of small, medium and large nests indicates a trend toward an increasing proportion of larger, older nests.

TABLE IV. — SUMMARY OF RECORDED INACTIVE NESTS.

DATE	NESTS WHICH BECAME INACTIVE	MORTALITY RATE PER YEAR
1931-1941 .....	168 (1)	5.0 %
April 1953-October 1953 .....	13	
October 1953-April 1954 .....	13	
April 1954-October 1954 .....	18	
April 1953-April 1954.....	26	8.3 %
October 1953-October 1954.....	31	9.5 %

older nests as indicated by the mortality distribution of the 44 nests which became inactive between April, 1953, and October, 1954.

NEST SIZE	NUMBER INACTIVATED	PERCENT OF OCTOBER 1953 POPULATION
Small .....	15	39.5 %
Medium .....	15	14.7 %
Large .....	14	11.4 %
	<u>44</u>	

(1) Represents only that number of the original 1931 population of 419 nests known to have become inactive, and not the total of nests inactivated during this time.

While 11 of these 44 nests were founded between April, 1953, and October, 1954, the remainder, 33, were established nests.

Of the 23 new nests founded in 1953, 4 died during the same year, mortality rate 17.4 %, and 3 died out in the following year, mortality rate 15.8 %. Of the 40 nests founded in 1954, 6 died in that year, mortality rate 15 %. Thus the mortality rate of newly founded nests, based on 63 nests, is approximately 15 % to 17 % in contrast to the 5 % to 10 % for the population as a whole.

Although the factors affecting mortality remain essentially unknown, below is a summary of available information:

FACTORS IN MORTALITY	NUMBER OF NESTS
Disturbance by man or domestic animals .....	6
Nest founded in an unsuitable location .....	1
Shaded by overhanging tree branches .....	7
Replaced by other species of ants .....	3
Unknown; no apparent external factors .....	27
	<hr/> 44

**Natality.** — The season and method of founding new nests has been discussed earlier. During the period of census, 20 new nests were discovered which were founded in 1953, and 43 which were founded in 1954. This difference is surprising, considering the fact that the population size remained almost unchanged. However this difference is probably due to more frequent and intensive searching for easily overlooked nests which are founded and become inactive in a few weeks during 1954, in contrast to 1953.

YEAR	RATE OF REPRODUCTION (NEST BIRTHRATE)	ESTABLISHED NESTS/NEW NEST
—	—	—
1953 .....	9.1 %	11.0
1954 .....	16.0 %	6.2

For this reason, the 1954 data are probably closer to the actual proportions for this population.

**Nest growth.** — The classic study of ANDREWS (1925), who measured the growth in size of a single mound nest of *Formica exsectoides* over a 19 year period, indicates that after an initial period nest growth in cubic feet accelerates, then depresses and finally attains a maximum size. After this, nest size decreases as the mounds become inactive and covered with vegetation. ANDREWS estimated the average life span to be 30 years, while DREYER (1942) calculated longevity at 25 years for mounds of *Formica ulkei*.

Nest size changes observed during the period of census are summarized in Table V. Further data are needed before growth rates for this population can be established.



TABLE V. — COMPARISON OF CHANGE OF NEST SIZE.

SIZE CHANGE	1931-1941		Oct. 1953-Oct. 1954	
	No.	%	No.	%
No change .....	104	24.8	206	78.3
Increase in size .....	116	27.8	24	9.1
Small to medium .....	41	9.8	18	6.8
Medium to large .....	47	11.3	6	2.3
Small to large .....	28	6.7	0	0.0
Decrease in size .....	31	7.4	2	0.8
Large to medium .....	19	4.5	1	0.4
Medium to small .....	8	1.9	0	0.0
Large to small .....	4	1.0	1	0.4
Died .....	168	40.0	20	7.6
Total .....	419		263	

### Summary.

1. Details of the life history, nest structure and 23 year population history are presented for an aggregate of mounds nests of the ant *Formica ulkei* Emery located near Chicago, Illinois, U.S.A.

2. There is a regular cycle of activity commencing in March and terminating in November. The mating flight occurs early in July, with the females returning to established nests after the flight. New nests are formed as buds of established nests.

3. Mounds nests are asymmetrically shaped with the long slope in the direction of greatest solar intensity. Alteration of the direction of greatest solar intensity by natural shading results in an alteration of the direction of the long slope.

4. The results of a population census in 1953 and 1954 are presented and compared with similar censuses of the same population in 1931 and 1941. Although the population size has not changed appreciably since 1941, there is a definite increase in the proportion of older nests.

5. Mortality rate is approximately 5 % to 10 % per year for the whole population, while for newly founded nests the mortality rate is 15 % to 17 %.

6. Population data are also presented on natality and on the growth of mound nests.

### Résumé.

1. On décrit ici une agglomération de nids en butte de *Formica ulkei* Emery qui se trouve près de Chicago, Illinois, aux États-Unis. On présente des détails sur le cycle biologique, sur la structure du nid et sur l'évolution des populations suivie pendant 23 ans.

2. Il existe un cycle régulier d'activité qui commence au mois de mars et qui se termine au mois de novembre. Le vol nuptial survient très tôt au mois de juillet et les femelles rentrent dans des nids bien établis après le vol. De nouveaux nids sont formés par bourgeonnement des nids anciens.

3. Les nids en butte sont de forme asymétrique et la pente douce est dirigée vers la plus grande intensité solaire. Le changement d'orientation du maximum d'insolation résultant d'un écran naturel produit une modification de la direction de la longue pente.

4. On présente les résultats de recensements de population de nids en butte faits en 1953 et en 1954, et on les compare aux recensements de la même population en 1931 et en 1941. Bien que la taille totale de la population n'ait pas changé d'une manière significative depuis 1941, il y a un accroissement marqué de la proportion des anciens nids.

5. La mortalité pour cette population est à peu près de 5 % à 10 % par année, tandis que pour les nids jeunes la mortalité est de 15 % à 17 %.

6. On présente aussi des statistiques de populations sur les nids nouveaux et sur la croissance des nids en butte.

### *Zusammenfassung.*

1. Einzelheiten der Lebensgeschichte, der Neststruktur und einer 23 jährigen (dreiundzwanzigjährigen) Bevölkerungsgeschichte einer Gruppe von *Formica ulkei* Emery Ameisenhaufennestern, die in der Nähe von Chicago, Illinois, in den Vereinigten Staaten von Amerika studiert wurden, sind in diesem Bericht dargestellt.

2. Das aktive Leben dieser Ameisen besteht aus einer regelmässigen und geordneten Aufeinanderfolge von Tätigkeiten, die im März beginnen und im November enden. Der Hochzeitsflug findet in den ersten Julitagen statt, und die weiblichen Ameisen kehren nach dem Flug zu einem bewohnten Nest zurück. Neue Nester entstehen durch die Tätigkeit der Ameisen in den bewohnten Nestern, die zum Teil Material ihrer alten Nester für den Neubau gebrauchen.

3. Die Haufennester sind unsymmetrisch geformt. Ihre längste Seite ist der intensivsten Sonnenstrahlung zugewendet. Wenn sich die Richtung der stärksten Sonnenstrahlung durch natürliche Schatten ändert, so erfolgt eine Änderung in der Richtung der längsten Seite des Haufennestes.

4. Die Resultate einer Volkszählung der Haufennester in 1953 und 1954 sind dargestellt und mit den Volkszählungen derselben Bevölkerung in 1931 und 1941 verglichen. Während sich die Bevölkerungszahl seit 1941 nicht bedeutend geändert hat, ist eine entschiedene Zunahme im Prozentsatz der alten Nester beobachtet worden.

5. Die Sterblichkeit dieser Bevölkerung ist ungefähr fünf bis zehn

Prozent jährlich, während die Sterblichkeit in den neuen Nestern fünfzehn bis siebzehn Prozent beträgt.

6. Ausserdem enthält der Bericht Information bezüglich der Entstehung und des Wachstums der Haufennester.

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# THE BEHAVIOR AND BIOLOGY OF CERTAIN NEARCTIC ARMY ANTS LAST PART OF THE FUNCTIONAL SEASON, SOUTHEASTERN ARIZONA \*

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Dr. Roy Whelden, Haskins Laboratory, Union College, kindly made available valuable information from his histological studies of the queens.

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## INTRODUCTION

Nomadism and a predatory, carnivorous life are characteristic of the known doryline ants. In tropical American species, emigration and related colony functions vary regularly in close relation to cyclic reproductive changes within the colony (22, 24, 27) rather than being irregular and dependent upon local food supply as was formerly thought (32, 16). There prevails in these species, throughout the year in both rainy and dry seasons, an unbroken succession of functional cycles, in which nomadic phases of high activity alternate regularly with stary phases of sessile life and low activity. This character of functional cyclicality depends upon massive stimulative effects exerted by the brood upon the worker population of the colony at specific recurrent stages.

Among doryline ants of the New World the genus *Eciton* in many respects contrasts strongly with the genus *Neivamyrmex*. Although *Eciton* is essentially tropical, ranging between 26° N and 26° S, *Neivamyrmex* extends widely into the North and South Temperate Zones from about 45° N in the upper Mississippi Valley to 45° S in Patagonia. Whereas *Eciton* has only 12 known species, *Neivamyrmex* has 113 (5) and possibly more. Numerous *Eciton* species are strongly epigaeic and even arboreal in raiding and nesting (29, 28); however, all *Neivamyrmex* species are hypogaeic in nesting and many in their raiding also. Workers, males and queens in *Eciton* are considerably larger than the corresponding castes in *Neivamyrmex*, the workers major in *Eciton* have large heads and huge hook-shaped mandibles unlike the smaller ones of *Neivamyrmex* workers, and other differences exist.

One striking difference between these doryline genera is that the essentially subterranean *Neivamyrmex* species range into the North and South Temperate Zones where their representatives have evolved under the conditions of an annual winter. The range of *Neivamyrmex* species is thus much wider than that of *Eciton*. The question thereby arises of what similarities and what differences may exist between *Eciton* and the Nearctic species of *Neivamyrmex* in their behavior patterns and related biological properties. This is the first of three studies designed to investigate representative *Neivamyrmex* species indigenous to the Northern Temperate Zone with respect to their adaptive patterns in comparison with that known for *Eciton*.

EARLIER RESULTS ON *NEIVAMYRMEX*

For an introduction to the biology of this ant genus, the publications of Wheeler (33, 35, 36), Emery (12), Bruch (9), Smith (30, 31) Borgmeier (5) and Creighton (11) may be consulted. It is clear from the literature that all *Neivamyrmex* species are essentially hypogaeic in contrast with species of *Eciton*. In the tropics their colonies are usually seen in or close to the forests or the gallery cover of rivers. However, Smith (31) notes for eastern areas in the United States that *Neiv. nigrescens* and *opacithorax* are not entirely subterranean, as their columns may be seen on the surface even in full sunlight. He states that in rugged country they are found in the valleys and on gentle slopes and plateaus but never on steep, exposed places.

Colonies of *Neivamyrmex* commonly nest in the soil, often beneath objects lying on the ground or partially buried. In the eastern U. S. their nests are often found in rotten logs and stumps and in the ground beneath these, and occasionally in or near the foundations of buildings (31). There is one report from Brazil of a colony of *Neiv. legionis* found nesting

7 m. up in a hollow tree (21), but even in the tropics nests of these ants entirely above ground may be rare. Observations of exposed *Neivamyrmex* bivouacs have not been reported, and in the tropics I have never found a colony of this genus whose nest was not very well sheltered.

In the central cavities of the nests of *Neivamyrmex*, clusters of workers are commonly found, as Wheeler (33) reported, "... in compact masses, often as large as a man's fist." Although this condition is confirmable for *Neiv. nigrescens* and *opacithorax*, other species may deviate. Under certain conditions, or perhaps typically, the occupied cavities may be enlarged by the digging operations of the *Neivamyrmex* themselves (8).

A seasonal adaptation of some kind would be expected in the *Neivamyrmex* of subtemperate and temperate areas, and this is indicated in Wheeler's (33) statement that in Texas,

"... during the winter and spring months, at least, the Ecitons (i.e., *Neivamyrmex* species) I have observed occupy the same nest. This they probably do until their young are raised."

Wheeler offered no evidence to support this statement clearly, and his suggestion of a time-limited raising of brood prior to a spring emigration is misleading. The possibility remains however that Nearctic *Neivamyrmex* species are characterized by an interruption of regular colony function under winter conditions, in contrast to species indigenous to the tropics and subtropics in which brood production and regular colony function may continue throughout the year.

The concept of long-continued nests ("Dauernester"), advanced by von Ihering (19) for *Labidus coecus* and accepted by others for *Neivamyrmex* species as well, suggests perhaps the maintenance of winter quarters. But the term as used by von Ihering and later by other writers seems to go beyond this. For example, Gallardo (14) reported a case discovered in the Sierra Ventana of Argentina, in which a colony of *Neiv. d'orbignyi* was unearthed at the same site in the spring months of two successive years. Although Borgmeier (5) considered this an indication that this species occupies *Dauernester*, such reports tell us only that colonies of the same species have been found in the same nesting place at different times. My records for doryline species in the tropics show for *Labidus* and *Neivamyrmex* as well as for *Eciton* spp. that not infrequently, in different years, different colonies may occupy the same nesting sites. In view of the question of a seasonal interruption of function in relation to possible statary phases, all claims for long-term doryline nesting must be examined carefully.

According to Smith (30), the colony populations of *Neiv. nigrescens* are "moderately large." Although no actual counts have been made, I estimate the worker populations of this species at between 150,000 and 250,000 individuals. Gillespie and Cole (15) describe the workers of *Neiv. nigrescens* as monomorphic and, from a measurement of 250 individuals, as having a size range represented by 0.52–1.50 mm. thorax

length \*. The worker population presents a smooth transition from largest to smallest, with the distribution skewed toward the latter. A series representative of the worker range is shown in figure 1.

In advance of the present study I hypothesized (27) for brood production and colony function in *Neivamyrmex* a relationship basically comparable to that found in *Eciton*. Support for this idea is found in my notes on emigrations of *Neiv. pilosus*, *sumichrasti* and *gibbatus* colonies in the tropics, in which great numbers of callow workers often thronged the columns. Also, information has been given to me for *Neiv. nigrescens* in



FIG. 1. — A physogastric queen of *Neivamyrmex nigrescens*, with a series of workers representing the range from maxima to minima. The queen was taken by Dr. W. S. Creighton on March 18, 1950, near El Salto, Durango, Mexico, from a colony found at 8,300 ft. bivouacked beneath a stone under an oak beside a meadow. Length of queen's thorax: 2.55 mm.

the U. S., in which large numbers of mature or nearly mature worker pupae were found, in one case (by E. Ross, in Georgia) in a highly active colony bivouacked under a log, in the other (by C. Rettenmeyer, in Kansas) in a colony which emigrated a few days after maturing worker pupae had been found in the nest. Present results sustain the hypothesis in detail.

Since Wheeler (33) reported the capture of a queen of *Neiv. opacithorax* in 1894 by Schmidt in N. Carolina and of *nigrescens* by himself in Texas, the collection of the queens of some 18 different species of this genus has been recorded. These captures, which have ranged from localities in Iowa and Kansas through the tropics to southern Argentina, need not be described in detail here. However, one fact of great importance to the problem of this investigation should be noticed, namely that about half of

\* However, Borgmeier (5) considers the *Neivamyrmex* worker series *polymorphic*. Although this point is subject to discussion, it is clear that *Neivamyrmex* workers are less strikingly polymorphic than those of *Eciton*.



the captures have involved queens in the contracted condition and the other half queens in the physogastric condition. This difference has been found through several species both in tropical and in subtemperate areas.

The taking of physogastric queens of this genus has been reported for 12 species, of which physogastry was incomplete at the time of capture in *Neiv. diana* in Brazil (2), *hetschkoi* in Argentina (9), *minense* in Brazil (2), *nigrescens* in Texas (33), and *raptans* in Argentina (7), and relatively complete in the queens of *angustatum* in Brazil (1), *humilis* in Costa Rica (3), *legionis* in Brazil (21, 9), *nigrescens* in Mexico (Creighton, pers. comm.), *opacithorax* in Tennessee (Cole, pers. comm.), *pertyi* (6) and *pseudops* (8) in Argentina, and *spinolai* (5) in Costa Rica. All of these queens were taken from subterranean nests. A transitional stage of physogastry, in the queen of *nigrescens* taken by Creighton, is represented in figure 1.

The taking of queens of this genus in the contracted condition has been reported for 13 species, which are: *Neiv. alfaroi* in Costa Rica (4), *carolinensis* in N. Carolina (13), *d'orbignyi* in Argentina (7), *gibbatus* in Panama (5) \*, *hetschkoi* in Argentina (9), *humilis* in Costa Rica (3), *nigrescens* in Texas (33) and in Mexico (20), *opacithorax* in N. Carolina (37), *pilosus* in Costa Rica (22), in Argentina (8), *raptans* in Argentina (7, 9) and *wheeleri* in Texas (10). With the exception of the queens of *gibbatus*, *pilosus* and *pseudops*, which were taken from emigration columns, all others in this list were extracted from the nests of their colonies.

From these results there remains little doubt that normally, as with *Eciton*, the colonies of *Neivamyrmex* spp. have only one functional queen. Among the many cases only three exceptions appear, that reported by Wheeler (33) concerning *Neiv. nigrescens*, by Bruch (7) concerning *raptans*, and by Bruch (9) concerning *hetschkoi*. In each of these instances two queens were found in the same nest, one laying eggs at the time. Here, much as in *Eciton* (26), it is likely that a colony with a mature sexual brood and undergoing fission is involved, with one queen (i.e., the one laying eggs) being the functional queen of the parent colony and the other or others virgin.

It is also clear from the above evidence that queens of many *Neivamyrmex* species may be found in either the contracted or the physogastric condition. The inference plainly is that these two conditions may arise at different times in the same queen, and perhaps alternately as I have found the rule in *Eciton* (23, 25, 27). The conclusion of various authors that contracted queens are 'young, not yet physogastric' would seem wrong as a generalization for this genus as it is for *Eciton* (24, 25).

The fact that in nearly all of a few dozen reported instances queens of *Neivamyrmex* species have been found either physogastric or contracted, with few in a transitional condition, indicates that queens of this genus,

\* The queen of *Neiv. gibbatus* reported by Borgmeier (5) was taken by Dr. R. Z. Brown, then my field assistant, from an emigration column at 11:00 p. m., Jan. 19, 1948, on Barro Colorado Island, C. Z. Large numbers of callow workers ran in the column, and a mass of excited workers formed a retinue for the queen.

like those of *Eciton*, produce distinct broods and are not continuously reproductive. This inference seems to find support in Holliday's (18) statement from her histological study of a partially physogastric queen of *nigrescens*, that

" . . . on the vagina occurred the receptaculum seminis of rather large size, apparently a necessary adaptation to the large number of eggs to be fertilized. That many of these are mature at a time is indicated by the fact that half of the tubules of each side contains several ripe eggs."

From her dissections, Miss Holliday estimated that the total number of ovarioles in the *nigrescens* queen "could not be far from 500." From a study of several queens of this species Dr. Roy Whelden (pers. comm.) finds this estimate conservative and judges that at the beginning of an egg-laying period each ovariole may contain an average of at least 10 mature eggs, and also many others in a series of decreasing size and maturity. A prolific reproductive capacity in this queen is indicated by results to be reported in this paper.

No systematic studies have been made on colony function in *Neivamyrmex*. The raiding forays of species such as *nigrescens* are carried out in columns, on chemical trails produced by the workers themselves (33, 31). Smith (30) states that the food consists largely of other insects, including termites, ants and their brood, and beetles. The colony diet, therefore, is essentially carnivorous (37). Smith reports that although ants of this genus tend to be predominantly subterranean (at least in their nesting), the columns of *Neiv. nigrescens* and *opacithorax* frequently appear on the surface, even in full sunlight. The inclusive pattern of colony raiding is unreported, and the relationship of foraging to emigration has not been studied in *Neivamyrmex* species.

## PROBLEM

Although it has been generally assumed that colonies of *Neivamyrmex* species, like those of other dorylines, have relatively temporary nests and are nomadic, no regularity has been claimed for their emigrations. The basis of their nomadism has never been studied, although we find the traditional food-exhaustion hypothesis accepted without question by Heape (1) and others. Smith's (30) statement that "The stays are governed largely by the availability of food for them" remains unsupported. On the other hand, by inference from my findings for *Eciton*, Creighton (11) has suggested that the movements of *Neivamyrmex* colonies may be regular and based on circumstances grounded in brood condition.

The first problem of the present investigation was to test the brood-excitation hypothesis for *Neivamyrmex*, favored over the food-exhaustion idea. To test the latter hypothesis, evidence was sought concerning

possible relationships between colony movements or failures to move and local food supply. In view of the brood-excitation hypothesis, evidence was gathered on brood condition in relation to raiding and to emigration, and laboratory tests were made to find what stimulative effects from brood might affect adults differently according to developmental stage.

If the favored hypothesis is supported, and Nearctic dorylines are found to have functional cycles comparable to those of *Eciton*, a second problem arises concerning the continuity of function in the colonies. Wheeler (33) did not find these ants active in the cold months, and it would seem likely that in contrast to the year-around cyclic function of *Eciton* a distinct winter break in function would prevail among dorylines in the Temperate Zones. Therefore the present study, the first of three directed at these problems, was scheduled for the latter part of summer in the hope of sampling colony function both in the regular season and in its possible autumnal changes.

### SUBJECT, LOCALITY AND CONDITIONS

The present study is devoted mainly to *Neivamyrmex nigrescens*, the species of this genus which is most widely distributed and most common in the Southern United States (31). This species is represented throughout a large area having mideastern North Carolina and midwestern Nebraska as its northern corners and southeastern Georgia and southwestern Arizona as its southern corners. The area of this investigation was southeastern Arizona near latitude 32° N, on the eastern face of the Chiricahua Mts. at an elevation of about 1,600 m. Also present in this area, and perhaps as common as *Neiv. nigrescens*, are colonies of *Neiv. opacithorax*, a secondary object of study in this research.

The investigation was carried out mainly in the vicinity of the Southwestern Research Station of the American Museum of Natural History in Cave Creek Canyon, from July 6th to Sept. 13, 1956. It thus extended from the height of summer into the time when nocturnal temperatures had begun their annual autumnal decline. Although during the summer in this locality nocturnal temperatures seldom fall to 10°C, after mid-August in 1956, by midnight superficial ground temperatures commonly had fallen below 10°C. and air temperature 6 cm. above the ground to 6-8°C, and in early morning hours the records were even lower. It is not just the latitude of the study area, but ecological conditions peculiar to the altitude and situation, that may be significant for the research. Due to factors related to altitude, the results may resemble more closely those obtainable under conditions farther north in the species range than those for colonies of these species living in zones at the same latitude but nearer sea level.

In the general locality, July and August normally are the two rainiest months of the year; however, in the 1956 season rainfall was unusually



light in August. Prior to mid-August, the Station area was reached nightly by convection currents of warm air rising through the canyon from the desert below. Although Smith (30) concluded that elevations of 2,000 ft. or less are optimal for *Neivamyrmex*, the described conditions holding in the area of the Southwestern Research Station may account for the fact that colonies of both *Neiv. nigrescens* and *opacithorax* were found to be relatively numerous there during the ten weeks of this investigation. Among other conditions favorable to many ants including these dorylines would be included a relatively good although scattered chaparral cover verging into pinyon-juniper and fir-pine associations, and a local geology contributing to a good retention of ground moisture. In addition to the ecological suitability of this area for the dorylines, insects and their brood serving as booty are also plentiful.

### METHOD AND PROCEDURES

The method involved longitudinal surveys of behavior and other functions in two or more colonies concurrently and cross-sectional surveys in



FIG. 2. --- Locale of the statary bivouac of Rock colony. A pile of stones in the central background marks the initial entrance point, to the right of which the colony nested in an area 1.2 m wide. In the foreground may be seen a section of the inspection lane surrounding the bivouac area; the string in the left background marks a principal raiding route.



other colonies over shorter periods of time, with samples of the brood taken regularly in each case.

In the first three weeks, during July, techniques were developed for studying individual colonies continuously. This involved procedures for tracing the routes of raiding columns and of emigrations with a minimum of disturbance to the ants, an exacting process when the columns ran for some distance under surface cover. As a rule, five surveys of each colony were made nightly,—one shortly after dusk, two others before midnight, a further one before 3:00 a.m. and a final one as appropriate before dawn. Records were taken of items such as activities at the bivouac, the direction and progress of principal raiding systems, and the direction and characteristics of emigration. For a protracted close study of activities, as when inspecting an emigration column for brood, a dim light was used,—otherwise five-cell headlights served for illumination.

To insure observing all columns and particularly emigration columns leading from the nesting site of a colony, a circular inspection lane was cleared around the bivouac center, at a distance of 5 m. or more as might be necessary to detect columns that started out by subterranean routes (fig. 2). This 'cordon' procedure was always used with statary colonies or with others operating under conditions of heavy ground cover. A physical continuity of successive emigrations was established in all cases of colonies continuously on record. After the schedule was standardized, the routine daytime inspection of colonies was minimized except on overcast days.

Brood samples were taken by removing specimens from the emigration columns with a suction bottle. These samples were fixed in Bouin's solution and preserved in 70 % alcohol. As far as possible, sampling was made nightly and was timed on each night so that the limits of the brood size range would be represented.

## RESULTS

### REVIEW OF PRINCIPAL COLONY RECORDS.

There follow summaries of the main facts concerning events in those colonies from which evidence was obtained bearing both on colony function and on brood condition. Each protocol is followed by a summary and interpretation.

#### *Pugsley colony, Neiv. nigrescens.*

On the night of July 12 a heavy emigration column thronged with callow workers, with a minimum of inert pupae carried, was discovered at 10:30 p.m. and observed until its end shortly after 1:30 a.m. White packets suspected to be early brood were also carried. From its origin near the base of a cement wall, the thick column meandered to the S 35 m. across an open area to enter a stone wall on the opposite

side, continuing its movement under cover for more than 25 m. to the *E* along this wall to a place where it nested for two days. Raiding was observed from this site on the three following nights, and on July 15 there were indications that at some time after 10:00 p.m. an emigration developed on raiding lines to the *SW*.

This colony is considered equivalent to colonies Lab-B, Thicket, Stone and Bridge, in that the first emigration of a nomadic phase occurred in the presence of a large, mainly eclosed brood of mature worker pupae.

*Meadow colony, Neiv. nigrescens.*

At 10:30 p.m. on July 15, the two basal columns of a large raid were traced across a field to the colony bivouac under a large stone (fig. 3). As had been observed in raiding colums in this area on the preceding night, the plentiful booty included both brood and winged forms of *Formica* spp. in particular. At 12:15 p.m. the *N* trail

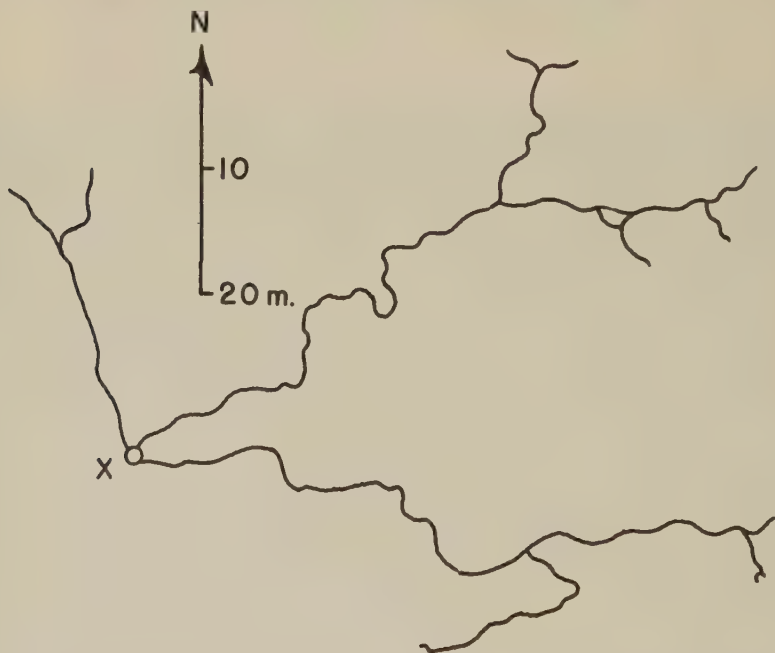


FIG. 3. — The principal raiding trails developed by a colony (Meadow, July 15) entering the nomadic phase, showing the origins of peripheral branches, after five hours of raiding when basal branches have died away. x, bivouac under large stone.

system had disappeared, and on the *SE* a wide outgoing column had pushed to a distance of 10 m. where it was then reversed by returning traffic. Overturning the bivouac rock exposed: 1) large windrowed masses of dark-brown adult workers with tens of thousands of light callow workers; 2) a new brood of embryos and a minority of microlarvae of potential workers in three main clusters, of which an estimated 95 % was captured for preservation; and 3) the queen, in a contracted condition, found in a rolled leaf in a mass of workers on one side of center. Captured for fixation were the

queen, most of the new brood of embryos and microlarvae (later numbered at close to 35,000) and perhaps 15,000 of the callow worker brood. Because of these collections, further events observed in this colony must be considered abnormal, but as such are of interest.

On the following nights, raiding columns issued variably from beneath this stone, but there was no emigration until on the night of July 20 the ants moved 21 m. to the *NE* into a stone wall. Here they remained, with nightly raids, until on July 24, after 8:00 p.m., a raiding line to the *E* was crowded with an exodus of workers and darkened callows. Larvae were transported after 10:00 p.m., but were few and a sample was difficult to obtain. There were branches after 40 m., but the most active raiding occurred from branches beyond 60 m. After 10:00 p.m. successive traffic reversals occurred, beginning peripherally, and increased in scope with time. Further reversals entailed increasing traffic disruption, with numerous rushing masses up to 12 cm. wide and often more than 2-3 meters long on the trail. At one collision point about 30 m. back from the raiding front, a mass of ants spread laterally from the trail in an eruption that surged more than 120 cm. upward on the trunk of a small tree. By 1:15 a.m. the reversals had expanded to include nearly the entire line to the old bivouac. (Reversals continued through the night, and only a part of the colony moved to a new site under a stone at 65 m.). On the next night an exodus again developed from raiding on this same line, after 10:15 p.m., with the entire (remnant) colony eventually moving into a stone wall at 70 m. from the bivouac site of July 17. Evening raids followed in this vicinity, with occasional abortive emigrations and one short completed emigration, until after the night of July 29 the ants could not be found.

—What might have been the first emigration of a nomadic phase was blocked by a major disturbance of the colony in which most of the young brood, a considerable part of the mature brood, and the queen were taken. The effect was to reduce further activities, and the absence of the queen evidently increased the difficulty of establishing new bivouacs on exodus, contributing to abortive and variable emigrations.

### *Rustler's Road colony, Neiv. nigrescens.*

At 10:15 p.m. on July 17 this colony had an unbranched column of workers to the *N* from their emergence point among leaves in a dry creek bed, following a meandering course 25 m. across grassy areas to a tree-root mound below which the main colony evidently was bivouacked. Many light-colored callow workers were seen in the traffic, largely directed toward the tree. A system of branching columns extended to the *NE*, and on the most active line from a stone road-fill at 55 m. much booty was lugged back to the bivouac. After 10:45 p.m., an exodus developed from the bivouac on this line to the road-fill area, with large numbers of callow workers running in the column and larvae (identified as potential males) in transport. The movement in wide column continued until after 3:00 a.m., with only booty carried after about 1:00 a.m. Traffic continued until dawn, thinly except for occasional bursts. On July 18, after dusk, there was raiding from the tree-mound on the same line, and after 8:00 p.m. an exodus developed in which further sexual larvae were carried. Interrupted for nearly an hour by rain, this emigration declined after 11:30 p.m. Efforts to trace the colony failed.

—This colony, with a large recently eclosed brood of callow workers and a young brood of sexual-form larvae, was judged to be in the first part of a distinct nomadic phase.

*Skunk Hollow colony, Neiv. nigrescens.*

On the night of July 20, this colony was located in a bivouac below stones near the creek, raiding to the *SW* more than 55 m in a complex of branches from a long base column. In a large cluster under one of the rocks, thousands of newly eclosed callow workers were clustered with adults. After dusk on July 21 there was a large raid to the *W* and across the creek. After 8:15 p.m. a heavy exodus developed on the base route, while raiding continued on peripheral branches to *N* and *W*. Newly eclosed callow workers thronged the base column, and many hundreds of larvae (potential males) were transported. Until 11:15 p.m. the emigration column ended at 35 m. where it entered a hole on the creek bank from which raiding columns diverged. Thereafter the wide column continued 30 m. farther to the *NW* on one of the branch trails to a preempted ant nest in the ground, the new bivouac. The queen, fully contracted, reached the new site with her retinue shortly before 3:00 a.m.; the emigration was completed shortly after 5:15 a.m. On July 22 after dusk the ants developed a raid to the *W*, with an exodus on the main line after 9:30 p.m. which at 25 m. stopped beneath a stone on the creek bank. After 12:30 p.m. the wide column continued across the dry creek bed under cover of leaves, and entered a hole on the opposite bank; soon reappeared, then disappeared beneath a large mass of brush. On the night of July 23, a thinner column followed the same line, completing the emigration although interrupted by rain. Within 30 min. after the heavy rain and rush of water down the creek, the ants had re-established their trail across the (now muddy) creek bed. The colony could not be traced through the thick grass of a boggy field which lay beyond.

—This colony, evidently beginning a new nomadic phase, was judged to resemble the preceding case as concerned behavior and brood condition.

*Laboratory-A colony, Neiv. nigrescens.*

From July 12, raids of *nigrescens* were observed nightly around the laboratory, extending in various directions from the rock fill. On July 22 after 9:15 p. m. a heavy emigration column crowded by newly eclosed workers passed to the *SE* from the laboratory to enter a mound 22 m. from the wall. Later in the movement, a young (potential worker) brood of embryos and microlarvae was carried in packets. On this and the following two nights the colony staged vigorous raids divergently from this site. However no further emigrations occurred until the night of July 25, when an extensive raid towards the *NW*, back into the laboratory rock-fill, was followed after 10:00 p.m. by an exodus in which callow workers (perceptibly darkened) as well as microlarval brood were observed, and the queen (contracted) entered the new bivouac at 12:15 p.m.

—After a succession of days terminating a statary phase observed at the laboratory, the colony started a nomadic phase by emigrating with a callow worker brood and an early larval brood to a new site which was occupied for two days without emigration. On the fourth nomadic day, in late evening, a further emigration ensued. It is probable that this colony moved away unobserved and that a different colony (Lab-B, below) was observed in the following period.



*Laboratory=B colony, Neiv. nigrescens.*

No raid was observed at the laboratory on the night of July 26; however, on July 27 columns were seen issuing from beneath the concrete steps on the *N* side of the building. On the following afternoon, which was overcast, after 2:00 p.m. a foray pushed from the concrete steps on the *W* side of the laboratory and branched into the clover field, advancing more than 30 m. by 5:00 p.m. Thereafter, on alternate nights, small raids or no raids were observed, until on August 2, which was overcast, a foray to the *NW* developed after 1:45 p.m. (fig. 4) and lasted until after 4:00 a.m. the following morning,

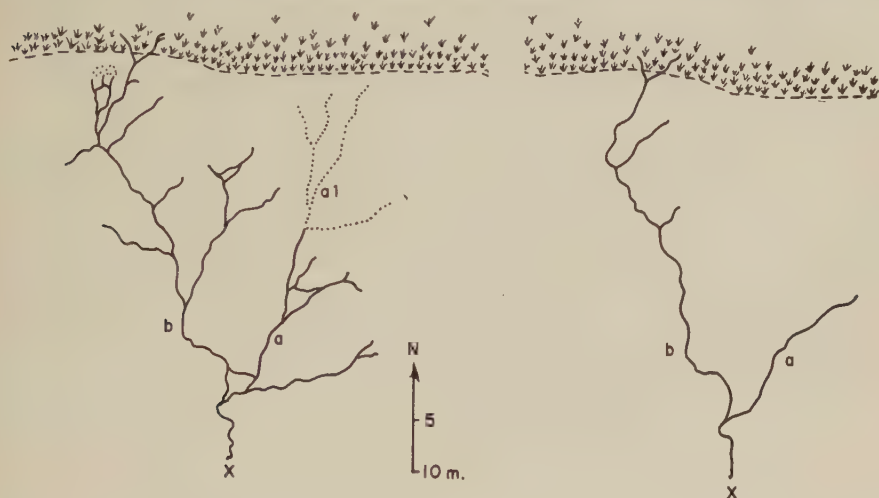


FIG. 4. — One of two trail systems of a colony of *Neiv. nigrescens* in the nomadic phase. *Left*, the trails set up at 9.30 p.m. after four hours of raiding, in which branch *a* is the older component (*a*<sub>1</sub> now in disuse), *b* the newer. *Right*, the same system at 11.30 p.m. with component *a* now mainly abandoned, *b* now followed by a single column branching profusely in a peripheral zone thickly covered by grass (upper area). *x*, exit from bivouac site in stone wall.

when a thin column still returned with booty. Only small nocturnal raids were observed until August 6, when on an overcast afternoon a foray pushed out to the *W* from a small hole in the *NW* steps used as exit in the three preceding night raids. Then at 3:30 p.m. a thick column was seen, crowded with newly eclosed callow workers, moving 10 m. over the rocks of the laboratory fill to disappear in its border zone. Although the heavy movement stopped at 10:30 p.m., the ants continued to raid during the night on branches probing into the rocks to the *S* of the stopping place. The young brood, doubtless in packets, must have been moved during a period when the observers were engaged elsewhere. On the nights of August 7 and 8, further raids occurred from the same site, extending base lines considerably into the open field to *SW* and *W*, but without an emigration. On the overcast afternoon of August 9 foraging columns extended into heavy grass; then after dusk an emigration began which carried the colony 45 m. to the *W* into a pile of rocks. On the night of August 10 one of three raiding forays led to the *N* into insect holes beneath some stones at 35 m. but no emigration was observed. This line was again in use on the following night, when a vigorous exodus developed to the stones and beyond, in which callow workers were numerous and the first sample of the current young brood was collected. The queen, contracted, passed after 12:00 p.m. Although for some time the ants carried their brood into an insect hole at 43 m., a resurgence developed, and by dawn most of the

colony had settled under stones at 35 m. Shortly after dusk on August 12, a strong exodus with brood carried the main part of the colony into the insect hole at 43 m., from which extensive raiding had developed from early evening to the NW and SW. The afternoon of August 13 was overcast following rain, and after 3:00 p.m. a foray developed to the NW on a previous trail across the open field, taking on much greater vigor at dusk. On this line a heavy emigration column developed after 7:00 p.m., with larval brood soon under transport and the queen (contracted) passing from the old bivouac site at 8:00 p.m. Although rain interrupted the movement at intervals between midnight and 2:00 a.m., the entire colony had transferred before dawn to a preempted ant nest in midfield (field site *x*). The afternoon of August 14 was overcast, and extensive raiding developed over a distance of nearly 40 m. to the *N* and *E* in the field. In the early evening booty was being returned on convergent routes to field site *y*, an abandoned *Pogonomyrmex* nest 25 m. to the *E* of site *x*; then after 8:00 p.m. an emigration developed on the base trail from site *x* to *y*. On August 15, overcast throughout, moderate raiding continued after 10:00 a.m. on lines to the *E* and *N* from *y*, mainly into ant nests in a grassy part of the field; much more vigorously after dusk. After 9:00 p.m., a variable exodus developed from *y*, and under stress of returning traffic resolved itself within an hour into a short transferral of the entire colony over an arcing course of only 2.5 m. to field site *z*, also an abandoned *Pogonomyrmex* nest. Throughout the night a booty-laden column continued its return to *z* from the NW. The afternoon of August 16 was overcast and, between rain flurries, traffic from *z* was observed. By 5:20 p.m. a vigorous column extended 25 m. to the *N* to a stone wall bordering the creek, with much booty carried back to *z*. At 9:30 p.m. a booty-carrying column had reached the wall from *z*; however, this column was reversed to *z* within an hour, no further exodus was seen and booty-carriers returned to *z* throughout the night. August 17 was overcast, and all day the ants were active bidirectionally on the trails from *z*, with a great increase after dusk. Evidently because of interruptions from rain, it was only after 12:10 p.m. that an emigration developed from site *z*, passing to the *N* into the stone wall. This movements, with larvae carried, continued until dawn, as did the return of laden foragers to the new site in the wall. On August 18, in the afternoon, extensive foraging was observed from the wall site into the well-shaded creek bed. By 7:30 p.m. a wide brood-carrying emigration column passed from field site *z* to the stone wall, with three large brood caches en route. After 12:00 p.m. this emigration column went on from the wall across the creek, with the booty-laden column now continuing on a previous raiding line across the lawn beyond to a new site (N-14), deep below leaves at the edge of a great rock near the road, more than 75 m. to the *N* of site *z*. This move had been completed by the entire colony before dawn. Although raiding developed promptly at dusk on August 19, it was not until after 9:00 p.m. that a brood-carrying exodus developed toward the SE. With many interruptions, particularly at advance trail-division points, this exodus finally traced a meandering course along the wall and across the lawn over a distance of about 40 m., taking the colony into a stone parapet (site N-15). The emigration continued until after 3:30 a.m., as did the return of laden foragers from the *E* and *N* to site N-15. On August 20, with overcast skies at 2:00 p.m. after a rain, a small foray was seen from site N-15 and from dusk extensive columns developed to the NE, soon mounting the bank to the road and dividing variously on the road and on the other side. Fortunately no automobile traffic disrupted these events, and by 8:30 p.m. the larva-carrying exodus had established a route across the road and up the steep rock face on the opposite side. At 10:00 p.m. the queen (contracted) appeared and was captured for fixation. The emigration was soon re-established, now terminating at a site (N-16) about 35 m. to the NE, under a great rock atop the hill. Because of the queen's capture, this colony thereafter was considered abnormal. However, due to an important relationship to Thicket colony that developed, a summary of subsequent events follows.

On August 21, in the evening, there was raiding to the NW and *N* from site N-16, but no emigration occurred. In the evening of August 22 complex movements developed, including extensive back-tracking across the road to site N-15; later, after

3:00 a.m., a movement with brood branched from the back-tracking route to a new site (N-18) 25 m. to the *W* of N-16. With trail-following again complicated on the evening of August 23, a resumption of the exodus with brood after 2:00 a.m. led beyond site N-18 to a new site (N-19) under an old stump. These movements continued on the evening of August 24, with raiding from sites N-16 and N-19, and an abortive back-tracking with brood to site N-15. Back-tracking was also observed from site N-15 to the *W* through site N-14 and to the *S* toward the creek, where a fusion with the Thicket colony (now also queenless) evidently was in progress. Throughout the night of August 25 these movements continued, with an extensive raid to the *N* from the stump, site N-19, where most of the colony was still located. During the night of August 26 there was a continued back-tracking shift toward the *S*, and a fusion with the Thicket colony. Although raiding continued from the stump on the hill (site N-19), after 12:30 p.m. there was an emigration with brood (now entering the prepupal stage) from the N-19 site to site N-18, and to some extent from the rock to site N-15 across the road. Throughout the night of August 27, as also on the night of August 28, these movements went on variably. The shift to the *S* kept going throughout the night of August 29, with a drift through site N-14 back toward the creek and continued fusion with the Thicket colony. After the night of August 26 there was no extensive shifting of brood (apparently still centered at sites N-19 and N-18) until the night of August 30, when a broad exodus column passed from site N-19 across the road to site N-15, carrying pupal brood as well as booty. On the following nights there were complex shiftings on the trails, with a drift into site N-15 and further junction with Thicket colony. On the night of September 3, all trails between N-13 and N-19 had thin variable traffic, but no brood was transported. After September 5, columns were seen nightly, emerging from beneath the Lodge (70 m. to the *W* of N-15). The fused Laboratory-Thicket colonies may have settled there before September 10, when nocturnal activities ceased in this area except for brief and limited forays in the early night.

—Periods A and B of the laboratory observations probably involved different colonies, but period B concerned only one colony. This colony at first completed a statary phase at the laboratory, with limited raiding, then entered a nomadic phase in which extensive nightly raiding was common and nocturnal emigrations were almost the rule. The nomadic phase began with the eclosion of a large brood of mature worker pupae, and as it continued a new brood of potential workers advanced from the microlarval stage toward the prepupal stage. The capture of the colony queen on the 16th day of this nomadic phase seemed to disrupt normal colony function. Instead of the three or four emigrations which might otherwise have occurred thereafter, prior to the attainment of early pupation in the brood, there ensued a variable backtracking and a more or less complete fusion with the Thicket colony.

#### *Creek colony, Neiv. nigrescens.*

At 10:30 p.m. on August 6 this colony was found engaged in a large raid and an emigration of more than 50 m. to the *N* from the South creek (see fig. 5). Raiding was interrupted and the emigration was delayed beyond a major trail division near the meadow by persistent major conflicts with three large colonies of *Iridomyrmex* sp. nesting there (points 2a, b, and c, fig. 5). By 12:00 p.m. most of a large recently-eclosed brood of callow workers had run the course from the old bivouac (r) to a cache beneath



a large rock at 2, and most of a brood of young worker larvae had been shifted to caches on the trail near 2. At 3:30 a.m. traffic was still variable around and beyond trail division 2, with indications that the emigration was continuing by degrees to site  $x_1$ . Later in the night, most of the colony moved with the broods to nest within a large wooden beam lying in the meadow (site N-6) about 64 m. from site  $x$ . At 8:15 p.m. on August 6 the emigration was completed by transportation to site N-6 of booty cached near the trail-division at 2, from which raiding continued during the early night. Also, from shortly after dusk a large raid had progressed from  $x_1$  to the SW across the field, with several major branches. In the early hours a large booty cache developed under a stone close to that under which the Meadow colony was

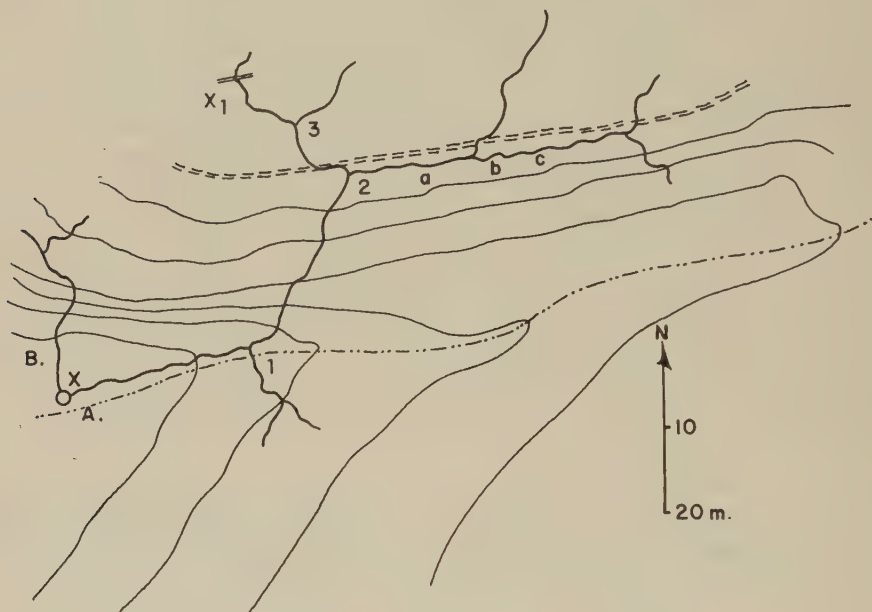


FIG. 5. — Sketch of two principal raiding systems (A, B) and the emigration route ( $x$  to  $x_1$ ) of a colony of *Neiv. nigrescens* (Creek, August 6) in the early nomadic phase. Explanation in text.  $x$ , bivouac of the day, under stone on creek bank, being abandoned as colony emigrates to  $x_1$ , new bivouac within a large wooden beam.

bivouacked on July 14-15, and a 15-m. section of former Meadow Trail to this site was in use. At 11:20 p.m. a booty-laden emigration column had developed from  $x_1$  to this point, 35 m. distant. Continued emigration beyond this cache was delayed by interference from traffic returning on several raiding lines converging here; however, after 12:15 p.m. the exodus pushed on to the W to the new site (N-7), a preempted ant nest under a stone on the creek bank, 63 m. from site N-6. A raid developed on the following evening on short lines to the E, W, and N, and booty-laden traffic returned to site N-6 until after 4:00 a.m., but no emigration occurred. The afternoon of August 9 was overcast, and raiding expanded beneath the leaves, reaching out more than 10 m. by dusk. Beginning shortly after nightfall, an emigration developed by stages through a complexly branched raiding system with numerous caches of brood and booty, to site N-9 about 46 m. to the SW of N-7. On two lines extending beyond N-7 to W and S, booty-laden traffic returned until after 5:15 a.m. The principal raid on the evening of August 10 extended to the W, and despite interruptions by rain an exodus carrying booty and brood had pushed farther along this line on the creek bank, nearing a



booty cache under a stone at 31 m. where the new bivouac (N-8) was established. To this site thin booty-laden columns returned until shortly after dawn. The afternoon of August 11 was overcast, and at 3:00 p.m. the ants were raiding to the *W* on several branching lines. Vigorous foraging in the evening initiated an exodus which by 10:00 p.m. had pushed out more than 40 m. along the creek bank, then bent sharply up to the *NW* on a branch trail where a brood cache was being established under a large rock. By 3:30 a.m. the exodus had pushed 15 m. farther uphill to the road-fill, on a peripheral trail in use at 10:15 p.m., to site N-9 at 47 m. from N-8. With low temperatures prevalent after dusk on August 12, the raid on complexly branched lines among the rocks near N-9 was almost entirely under surface cover, and no emigration took place. A continuation of raiding on some of the same base-lines after dusk on August 13 led into an emigration to the *SW* which ran beneath rocks through nearly the entire course of 51 m. The new bivouac site (N-10) covered more than 1 sq. m. in insect nests below adjoining rocks. Although this general area, a high creek bank, was rock-covered, vigorous raiding developed only after dusk, with few indications of daytime raiding. In the evening emigration of August 14, a distance of only 8 m. was covered (to site N-11) in several stages of brood-shifting from one to the next of three caches beneath large rocks, with signs of extensive feeding of larvae. Just before 10:00 p.m. there was a lasting reversal of the exodus by rain. The evening emigration of August 15 carried over a distance of 30 m. to site N-12, again with a relaying of larval brood through two or more intermediate cache points at which brood-feeding occurred. After dusk on August 16 there were indications of raiding among the rocks on numerous relatively short divergent lines, with much shifting of brood under rocks around the bivouac site, but without any emigration. The afternoon of August 17 was overcast, and short raiding columns from the bivouac were observed. Raiding became much heavier after dusk with much booty returned during the night. A heavy exodus to the *E* began about 2:00 a.m., but was soon reversed and there was no emigration. On the evening of August 18 a brood-carrying column was observed working its way to the *E* and *NE* through the raiding zone, ending at 11:10 p.m. in a large brood cache beneath rocks at 45 m. Still moving at 4:00 a.m., this column then led under a large rock (site N-15) 3 m. farther on, to which laden foragers returned in two converging lines. Raiding after dusk on August 19 continued the development of one of these lines uphill at angles to the *N* through the rocks, and an emigration which developed on this line after 9:00 p.m. followed almost the exact route taken by this colony in its downhill course on August 13. The movement carried over a distance of 58 m. to site N-16, close to the site occupied on August 11-13. Next afternoon, digging disclosed that the colony had its nearly mature larval worker brood packed into the many chambers of an abandoned ant nest, to a depth of more than 50 cm. below a large rock. The disturbance may have stimulated an earlier exodus that evening, leading across Rustler's Road into a raiding zone on the opposite bank. At 4:00 a.m. the emigration ended there with the new bivouac (site N-17) established beneath some large rocks. The night of August 21 found the colony raiding until after 4:15 a.m. on numerous short lines beneath many rocks near the bivouac, and some shifting of brood was observed (probably with brood-feeding), but no emigration took place. Development of the *NE* raiding system continued from dusk on August 22, and after 10:15 p.m. an emigration developing on the principal trail in this direction carried nearly 40 meters uphill to the exposed entrance of an ant nest on the rocky slope. This emigration continued after nightfall on August 23 and was completed shortly before 1:30 a.m., with the transport of the remainder of the brood, now mainly or entirely in the early pupal condition.

The colony remained at this site until Sept. 4, with no raids observed on the nights of August 24 and 25, and September 1, and relatively small raids on the other nights. The successive forays all developed rather slowly and variably, emerging from different insect holes within a radius of 4-5 m. A small raid to the *E* on the night of September 4, extending a route used on the preceding night, changed at some time

after 11:00 p.m. into a heavy emigration across the bare hillside into an insect hole under leaves at a distance of 23 meters. A large brood of only faintly pigmented worker pupae was carried in the column, but no young brood was seen despite a close watch. The queen, followed by a large retinue of workers, appeared in the column shortly after 1:00 a.m. Nearly maximally contracted, she was collected at once for fixation. (This unforeseen event displaced a plan to dig into the bivouac on September 7 to capture the queen and inspect the brood.) The colony remained at the new site, with weak nocturnal raids, until it was last visited on the night of September 12.

—When this colony was first seen, it was then at about the 5th day of a nomadic phase, judging from the pigmentation of the callow-worker brood and the size range of the larval = worker brood. Nocturnal raiding persisted at a fairly high level, with emigrations ensuing on most of the nights, as the young brood passed through its larval stage of development. When most or all of the brood had reached the early pupal stage, the colony entered a statary phase of low raiding activity and without emigration except for the movement which occurred on the night of September 4. The colony otherwise evidenced a low excitement level in the entire period following August 23, and this movement may have been due to an exceptional disturbance (see Note 4). It is probable that raiding would have increased considerably in vigor and the colony would have emigrated soon after September 12, or when the pupal brood had matured fully. The non-physogastric condition of the queen, together with the absence of eggs, indicated a failure to deliver a new brood at the predicted time midway in the statary phase.

### *Bridge colony, Neiv. nigrescens.*

This colony was first observed at 11:40 p.m. on the night of August 9, engaged in a large raid and in an extensive emigration to the *E* in the lower dry creek bed. A potential all-worker larval brood was carried in the column, or heaped with booty in one of numerous large caches. At 12:50 p.m. the emigration column, moving through the advanced zone of raiding, led to a log in a boggy area. At 1:00 a.m. a large cluster was visible in a 7 cm. high space beneath this log, into which the emigration column emptied; however, the emigration later continued 12 m. to the cement pier of an old footbridge within which the colony settled. On the following three nights there were moderately developed raids, but no emigrations. The raid of August 12 was completed before 3:00 a.m. Next evening, in the course of a larger raid, a heavy brood-carrying emigration column moved to the *S* across an open grassy area. At 8:00 p.m. the first brood-carriers had reached a point 25 m. from the old bivouac, and at 9:00 p.m. the colony was settling beneath a pile of logs. With one lengthy interruption by rain, the emigration continued until after 5:00 a.m.; then to the *NE* raiding had ceased, but ants were still returning from the *SE*. August 14 was somewhat overcast, and at 10:30 a.m. thin columns extended to the *SE* from the bivouac. A large raid developed that evening to the *SW*, and at 8:30 p.m. a vigorous emigration column extended 45 m. to where the ants were entering an insect hole beneath a stone. Several short raiding branches with terminal swarms extended from this point under the dry leaves. On the following night, after raiding began, emigration occurred similarly, arcing *SE* to a trail division and brood cache at 25 m., and by 1:30 a.m.

extending to a point on the stony hillside at 35 m. where a large cluster and brood cache had formed under a rock. At 4:30 a.m. the emigration extended to a rock 3 m. beyond the previous point, with brood being deposited in a large booty cache there. On both of these nights, nearly the entire emigration passed beneath leaves and other ground cover. Extensive brood shifting beneath the rocks occurred on the next afternoon. This action continued in the evening, and around 10:00 p.m. an emigration started to the *NE* on the most vigorous line of raiding, running along the contour into a cavity below a stump. The raid of August 17 was a large one, and by 11:30 p.m. an emigration column had developed through the *E* trail system uphill and along the sharp crest. By 2:00 a.m. the larva-carriers had reached a point in the upper meadow at which an insect hole was entered, as raiding continued beyond. With several brood caches forming, the emigration continued until nearly 6:00 a.m., when it led on to a site beneath a rock at 35 m. On the afternoon of August 18, with overcast skies, a thin emigration column continued on this route. At 10:00 p.m. this emigration was vigorous, and on the larger of two raiding systems from the new site, a brood-carrying emigration column passed on 40 m. to the *NE* to a similar bivouac site on the stony plateau. At 3:30 a.m. the resumed emigration from the site of August 17 had ended, but the advance exodus ended beneath a stone at a tree 3 m. from its former terminus. At 10:00 p.m. on August 19 the pattern of the previous evening was approximated, with both continued emigration from the old site and an advance emigration to the *E* through the principal raiding system to a new site beneath some rocks in a little draw. At 3:45 a.m. this emigration continued, but all raiding had ceased. On August 20, although a vigorous raid developed in two directions after dusk, emigration was limited to a shifting of brood over a surface distance of only 3 m. This movement continued at 3:45 a.m. after all raiding apparently had ended. There was no emigration on the night of August 22, although forays developed on short lines in various directions. All ants had returned by 3:45 a.m. The principal raid of August 23 evening was to the *E*, and after 8:00 p.m. an emigration developed through this system, over an arcing, irregular course. At 3:45 a.m. this movement continued to the new bivouac site, an insect nest under stones at 76 m., with a heavy return to this place on two advance raiding lines. At 8:05 p.m. on the following night a continuation of this emigration was in progress, with one very large brood cache under a stone 15 m. from the bivouac of August 23. This movement was completed by 1:15 a.m. without any further advance beyond the site occupied by a part of the colony on the preceding night. At the time of this final transfer, the brood had entered the early pupal stage.

The colony remained at this site during the following 18 days, in which only relatively small raids developed on most of the nights, but without forays on the nights of August 31 and September 8. The successive raids led off in different directions from different exit holes scattered within a radius of 3 meters. The forays of September 9 and 10 seemed to be more vigorous and extensive than any others of this period.

The first evening foray of September 11 was a moderate one to the *W*, the second was a stronger outburst arcing to the *NW*, and on the line of the latter a vigorous emigration developed after 8:00 p.m. The column was thronged with callow workers, all at first running independently, but after 8:30 p.m. with a minority of them inert and transported. The queen (fully contracted) appeared at 10:20 p.m. followed by a long retinue, and was collected for fixation. The thick column including callows stopped shortly after 12:00 p.m., when the temperature 5 cm above the ground was 8.7°C and within the surface soil 14.5°C. The emigration was completed on the following evening. In the entire movement, no brood was found except that of mature pupal workers.

—Judging from the condition of the brood, this colony when first discovered had reached the seventh or eighth day of a new nomadic phase. This phase continued with the further maturation of a larval worker brood and ended when this brood attained the early pupal stage.



The colony then entered a statary phase, with only small raids and no emigrations until the current brood reached pupal maturity. In the emigration coincident with that change in colony condition, no young brood was found.

*Thicket colony, Neiv. nigrescens.*

On the nights of August 17, 18 and 19 columns seen raiding in the upper creek area were differentiated from those of the Laboratory-B colony and were traced to the *SE* cement post of the footbridge. The evening raid of August 22, which was much more extensive than before, originated from the *SW* post of the bridge, and expanded mainly across the field recently vacated by the Laboratory-B colony. By 9:25 p.m. a broad exodus developed on this line in which a mature pupal worker brood appeared, most of it inert and transported by adult workers. For several hours this column discharged into a small hole, the entrance to a preempted ant nest, near a trail division point 38 m. out in the open field. The queen, fully contracted, appeared at 10:50 p.m. and was collected for fixation. After 12:00 p.m. small packets of new brood began to appear in the column, and continued although sparsely until the end after 1:00 a.m. Despite a continuous watch, only about 2,500 pieces of such brood were taken, very small in numbers for the species. After 7:15 p.m. the following evening the exodus continued on the same line, with callows numerous, now most of them running independently. No young brood was seen in this movement, which after 3 hours was replaced by a thin, variable line between the bridge and field nest, thereafter a continuous feature at night. This and further behavior was considered abnormal.

Back-tracking continued on the following three nights, when moderate raids developed from the field nest to the *W* and *S* particularly, but without emigration. After 9:00 p.m. on the night of August 27 the column thickened to an exodus from the field nest to the *SE* bridge pier. This column, crowded with callow workers, first entered the pier, then continued across the creek bed on an old raiding trail of this colony which crossed various known trails of the Laboratory-B colony. (A close watch was kept for young brood, but less than 250 microlarvae were taken.) Through this complex of trails, ants from the Thicket colony reached and entered the same small hole in the cement wall used by the Laboratory-B colony (N-15) one week before, at a site now occupied by part of that colony. A fusion of these two queenless colonies, evidently in prospect, was indicated on the following nights by the presence of occasional callow workers (which could only have come from the Thicket colony) in the lines on the hill to the *N* of the road, between sites N-16 and N-18 of the Laboratory-B colony. A widespread following of these and related trails by the continuous columns of these colonies, undergoing fusion, was observed on the following nights until September 12.

—This colony was found during the last week of a statary phase, and its queen was captured on the first emigration of the succeeding nomadic phase, when a large eclosing worker brood was present. There was also a new brood, but its numbers seemed unusually sparse for the species. There was no further emigration until three nights thereafter, when an extensive movement on the back-trail carried this colony into fusion with the Laboratory-B colony, also queenless.



*Rock colony, Neiv. nigrescens.*

When found on the night of August 26, this colony was engaged in a vigorous raid of two trail systems mainly to the *W*, and bivouacked under a large rock in a grove about 400 m. to the *E* from the current site of the Creek colony. No emigration occurred, despite lengthy eruptions at two different times. At 6:00 a.m. next morning, thick columns were still returning to the bivouac with booty, including adults and pupae of *Formica* spp. in particular. In the course of a large raid on the following night, mainly on two systems to the *SW* and *NE*, an emigration developed after 11:00 p.m. in which a large brood of early pupal workers was transported. The movement progressed by stages through two or more caches under rocks, into a preempted nest of fungus-growing ants under the rocks at 14 m. The raid of the following evening, although at first heavy, fell off sharply after 10:00 p.m. and no emigration occurred.

The colony remained at this site (fig. 2) with relatively small divergent raids on some of the nights (and no raid on August 31), until it was excavated on September 4. Its nest, about 1 m. broad and nearly as deep, occupied most of the galleries and chambers of the dispossessed myrmecine colony, the remnants of which huddled in peripheral chambers. Below a surface layer of dry soil about 12 cm. deep, the dorylines were clustered thickly with their pupal worker brood in several dozen chambers distributed through a thick root mass in light, humid soil to a depth of about 95 cm. The queen, nearly maximally contracted, was found near one side about 30 cm. down. A thoroughgoing search of the entire nest disclosed no eggs or other young brood. When last seen on the night of September 11 the colony was still clustered with its pupal brood under stones at the bottom and one side of the excavation, and had a thin single column over the parapet to the *E*.

—This colony when found was completing a nomadic phase, with an all-worker brood at the early pupal stage of development. After one week in the statary condition, its nest was excavated so that the queen could be captured and the brood thoroughly inspected. As no brood other than the one then in the mid-pupal stage was found, and as the queen was non-physogastric, although the colony would have emigrated from this site on the eclosion of the advanced brood, a continuation of nomadic function would have been doubtful.

*Stone colony, Neiv. nigrescens.*

When discovered on the night of August 30, this colony was raiding on a long, branching trail-system extending more than 30 m. to the *E* from its bivouac in an old foundation near the upper spring. Next night there was a relatively light raid to the *NW*, and on the night of September 1 a somewhat heavier raid to the *W*. On September 2, at 8:15 p.m., a full emigration column meandered through leaves and stones 35 m. to the *W* on the principal trail of the previous evening's raid. In this column, for several hours, light-colored callow workers predominated, with a relatively small proportion of mature worker pupae carried by workers. Despite a continuous inspection of the column, there was no sign of young brood. The queen (contracted) was permitted to pass in this movement, but was taken for fixation when she passed at 9:05 p.m. in the next emigration, on September 5. Raiding on the evenings of September 3 and 4, although rather heavy, was relatively limited both in distance and in duration. At one point in the latter raid, a mass 1 m. wide operating in vines

and brush spread upward over the trunk of a large juniper tree for a distance of nearly 2 m. Back-tracking began after 8:00 p.m. on September 6, and somewhat later a wide emigration column thronged with callow workers surged back for 20 m. toward the first nomadic bivouac. During the following three days the colony remained in the vicinity, with a short emigration on the night of September 8, first back-tracking, then reversed toward the site of September 5. At 9:00 p.m. on September 9 a mixed column was seen back-tracking from the first nomadic bivouac; however, on the following nights the ants could not be found in the vicinity.

—This colony was observed during the last 3 days of a statary phase, also in the first four days of a nomadic phase which ensued on the eclosion of a large pupal worker brood. The case resembled the Rock, Creek and Bridge colonies in that no young brood was found at the time. The failure of emigration on the second and third nights of the nomadic phase was not unusual under the conditions; however, back-tracking and difficulty in resettling observed on the following nights, as with the Meadow colony, was attributed to the removal of the queen.

### ***Lodge colony, Neiv. opacithorax.***

On the night of July 12, when this colony was found at the Lodge, at 3:00 a.m. a heavy column emerged from a short flight of stone steps and moved along the base of a stone wall for 3 m. in the open and then into the wall, transporting a larval (sexual-form) brood. This movement continued past 5:00 a.m. After 8:00 p.m. on July 13, a bidirectional column was first seen, then a thicker column 8-10 mm. wide transporting brood as on the previous night. This column was traced 15 m. to the *N*, reappearing three times from the stone wall before it disappeared into thick grass. Traffic thinned out after 11:00 p.m.

—This colony was nomadic, with a large brood of sexual-form larvae.

### ***Spring colony, Neiv. opacithorax.***

On August 8 at 11:00 p.m. this colony had a complex raid on trails branching to the *SW* in the field beyond the upper spring, and a long meandering emigration column extending 40 m. to the *NE* where a large cache of brood and booty was found beneath a stone on the creek bank. Thousands of potential worker larvae (range 0.58-3.6 mm.) were transported in the column.

—This colony was nomadic, in a highly vigorous condition of activity with a potential worker brood well advanced toward larval maturity.

## **RAIDING**

In the locality of this investigation, the raiding columns of *Neiv. nigrescens* usually and of *opacithorax* always issued at dusk and foraging continued during the night, often to dawn. In the former species there

were relatively few exceptions save on overcast days, when raiding sometimes occurred but then very subdued in comparison with nocturnal forays. At rare intervals in this species, usually when a colony was highly excited as in the presence of a newly eclosed worker brood, raiding might occur in full sunlight. This generalization holds for the area of study, in which a mixed cover seldom held light at ground level to a low intensity except on overcast days. In contrast, in the forests of Central America, Mexico, and Trinidad I have frequently observed vigorous daytime raiding in *Neivamyrmex* species such as *pilosus*, and at times over a considerable area.

Two principal conditions of raiding may be distinguished, that of a colony in the *nomadic* condition and that of a colony in the *statory* condition. Nomadic raids tend to begin earlier, usually as dusk approaches, involve much greater numbers and more branching columns generally with larger terminal groups, and are usually characterized by an emigration over one of the principal raiding trails. Raiders from a nomadic colony tend to be much more excitable than in a statory colony so that outbursts generally are stronger and more lasting. The evening exodus from a statory colony typically holds its peak only for a few minutes, after which the basal column is thin until the laden return begins. In contrast to the reduced level of statory colonies, the output of a nomadic colony may remain at peak for two hours or more, and in the periphery greater numbers usually are brought to bear more quickly upon any excitation center at which new booty is found or stiff resistance is met. In the latter, persistent excitement is greater on trails both in the raiding front and in the rear than in the former. Raiders from a nomadic colony generally take a larger proportion of adult insects such as ant workers and sexual forms, beetles and the like, than those from a statory colony, of which the booty tends to be the soft-bodied brood mainly of ants.

In the less frequent instance when a colony of *Neiv. nigrescens* has settled at or beyond the limit of its previous raiding zone and new, unworked territory confronts it, a characteristic pattern of initiating a foray is observed. Ants then crowd out in several directions, and as this mass advances it splits variously and is succeeded on the same terrain by a network of columns and finally by branching columns (fig. 3, 4 and 5). Orientation is chemotactical, and, as the zone of raiding is extended, anastomosing columns remain of which the strongest radii continue to follow chemical traces behind the advance. In figure 4 one trail system of a nomadic colony is represented as observed about four hours after raiding began at dusk. Dotted lines in the periphery of system *a* indicate trails abandoned as heavier booty found elsewhere drained ants from the area first exploited. In the sequel, sketched 90 minutes later, and after a rain, system *b* is now abandoned but *a* has entered a zone thickly covered with grass, where the raid advances with a profuse branching of columns.

The raid of a colony of these *Neivamyrmex* species thus advances in



three stages: 1) spreading groups in the forefront, succeeded by 2) areas of dividing, anastomosing columns and finally 3) a single long base column with terminal branches. The advance groups may be anywhere from a few centimeters to a meter or more in width, their survival as masses in given terrain depending particularly upon the intensity of raiding and the local booty supply. Usually, as the sketches shown in figures 3, 4, and 5 indicate, secondary branches disappear from use in the course of time and only the base trails remain in use. The pattern of nomadic raiding systems varies according to the topography and the distribution of booty. Two large branching-trail systems, each with its principal or base trail leading from the bivouac, may remain in use for hours, one of these may disappear and a new one develop, or one alone may persist. The advance from the bivouac may be slow or rapid according to conditions, and after some hours may extend only 30 or 40 meters with numerous long branches or more than 60 meters with fewer branches in use.

Similarly, although on a smaller scale, the raids of *Neiv. opacithorax* involve one or more systems of columns on branching chemical trails.

Storage heaps or caches of booty usually develop at trail branches in the zones of more productive raiding. In these the booty may be left for hours, heaped under cover, before it is removed to the rear or forward depending on how the emigration develops. In the raid of the Creek colony on the night of August 6, represented in figure 5, an early cache under a small stone at junction 1 was removed and smaller ones at 2a, b, and c disappeared before 11:30 p.m. as the emigration moved forward, but a large one at junction 2 remained throughout most of the night.—When in the route of emigration, booty caches may also become temporary depots where larvae are deposited and consequently where extensive feeding can occur.

Under the conditions of this investigation, the regular, extensive raids of this species occur at night, and raiding columns were not seen on the surface in the daytime except on overcast days. When a colony is in a highly excited condition, as at the beginning or near the end of a nomadic phase, subterranean raiding may occur to an appreciable extent in the daytime, although as a rule only relatively close to the bivouac when subterranean channels are available. It is unlikely that these ants usually get out very far from the bivouac except at night, and then only on the surface or under ground cover such as leaves and stones. At times large sections of a raid or even an entire raid may be active beneath surface cover. The columns tend to run along beneath objects such as fallen limbs rather than on the upper surface, as is common with the columns of *Neiv. pilosus* and others in tropical forest. As an exception, when the Bridge colony was raiding in a boggy area on the nights of August 10, 11 and 12, its columns often followed the tops of logs and fallen limbs; however, in a dry area on the following night, the columns ran below limbs and the raid largely developed under leaves and other ground cover. These ants seldom leave the ground in their raiding, and then as a rule



only when considerable numbers surge forward simultaneously in a limited space, as with the Stone colony on the night of September 4.

Under statary conditions the raids are smaller and less vigorous than in nomadic colonies, and on some nights raiding is brief or absent. The raids on successive nights then tend to be in different directions, although at times, after intervals of disuse, the same base route may be extended. The various routes taken by the Creek colony and by the Bridge colony during their statary phases were roughly axial from the bivouac center, although few forays of the former colony mounted the steep hillside, and none of the latter probed far into two sectors evidently deficient in booty.

### THE QUEEN OF *NEIV. NIGRESCENS*

Morphological studies by Holliday (18) and Whelden (pers. comm.) on the queen of this species indicate that a large number of eggs may be matured at one time. In this study the number found in one distinct brood, that of the Meadow colony, was more than 37,000. Judging from the earliest brood ranges obtained (*i.e.*, at the outset of the nomadic phase) a few days and probably not more than one week suffice for the actual laying operation. A short-term output of this magnitude would not have been suspected for the relatively diminutive queen of this species, whose total body length with contracted gaster is only 12-14 mm. Under the conditions of this investigation, the interval between broods was about 30-35 days. As in *Eciton*, a succession of all-worker broods is the rule, and sexual broods appear to be exceptional.

The queen remains in the nest except for the time when she runs in the emigration column to a new bivouac site. This event, described by Reichensperger (21) for an emigration of *Neiv. pilosus* witnessed in Costa Rica, was observed many times in this investigation. The queen's passage always occurred at night and in all cases she ran the full route under her own power, moving along steadily with a thickened column of highly excited workers pressing around and after her. Although the workers are strongly attracted to the queen and greatly excited when in her vicinity, they seldom run over her in the emigration to the extent that she is hidden from view, as is common in *Eciton burchelli* and frequent in *hamatum*.

Seven queens of *Neiv. nigrescens* were captured and preserved in Bouin's fixative for histological study by Dr. Whelden. With the exception of the Meadow queen, collected for evidence on the queen's condition in relation to brood in the regular season, all of these queens were captured late in the project. With the Meadow queen two broods were found, one potential worker brood in the embryonic and microlarval stages, and one callow all-worker brood, mainly eclosed. Both of these broods may be attributed to the function of the one queen, and the spacing may be considered representative. From Dr. Whelden's findings, this queen,

contracted maximally when taken, would have produced a further brood in due time.

The remaining six queens were taken when the work was in its last stage, two (Thicket and Bridge) for additional evidence on the queen's condition at the beginning of the nomadic phase, one for her condition early (Stone) and one late (Laboratory-B) in the nomadic phase, and two for her condition before (Rock) and after (Creek) the time hypothesized for regular egg-laying midway in the statary phase.

In this queen series there were major departures from expectations. All of these queens were maximally contracted or nearly so at the time of capture. In strong contrast to the Meadow queen, of the two other queens taken at the outset of a nomadic phase only the Thicket queen had produced a new brood, and this was found abnormally low in numbers. But neither Bridge nor Stone, when the queens were captured early in September as a nomadic phase began, had any young brood so far as could be ascertained. As for queens in the statary phase, both the Rock and Creek queens were nearly maximally contracted when taken, and in neither colony were any eggs found, despite a careful search in the excavation of the Rock statary nest and a close watch on the sporadic emigration of Creek colony. From the presence of a maturing pupal all-worker brood, it may be inferred that in the preceding statary phase both of these queens had passed through physogastry (fig. 1) and egg-laying.

From his histological studies of the last six queens, all taken after August 20, Dr. Whelden found no indication that any one of them was maturing a new brood. However, from the results on regular colony function and reproduction earlier in the season, the Rock queen should have been physogastric and laying or nearly ready to begin laying eggs, the Creek queen should have completed or nearly completed the laying of eggs, and the Thicket, Bridge, and Stone queens should each not only have laid the eggs of one brood within about two weeks previously, but also should have entered the early stages of producing a further generation. The results support the conclusion that although all of these seven queens had been normally reproductive at least up to times within a few weeks preceding their capture, a termination of reproduction had set in for every one of them, except the Meadow queen. For the Thicket queen, what would probably have been her last brood of the season evidently was curtailed. These and other considerations indicate that this period marked a termination of reproduction for the current year in these queens and their colonies.

The workers of *Neiv. nigrescens* are strongly attracted to their queen. This is indicated by observations of behavior on the emigrations, of worker responses to queens temporarily housed in laboratory nests or to queens returned to their colonies after detention periods up to 24 hours, and (in the cases of the Meadow and Rock colonies) of clustering responses observed in the nests. A further fact indicates the major role played by the queen in the unified function of her colony.

This concerns the response of a colony to an absence of its queen exceeding about twelve hours. After the Thicket, Stone and Laboratory-B queens had been captured, in each case a definite back-tracking on earlier emigration trails was seen on the following night and two or more nights thereafter. Such behavior seems attributable to the effect of the queen's protracted absence, as it was not otherwise observed in nomadic colonies of this species. Also, as indicated in the colony protocols, an abnormal pattern of behavior appeared in the Meadow colony, and in the Stone and Laboratory-B colonies as well, in the form of a difficulty to establish nest sites in the course of back-tracking emigrations. No back-tracking was observed in the Rock and Creek colonies, which were statary when the queen was captured, and the Bridge colony was not observed on the nights following the queen's capture.

There is no indication that normal (*i.e.*, queenright) colonies of this species are likely to fuse. However, the cases of the Thicket and Laboratory-B colonies indicate that under certain conditions, when back-tracking leads one colony into the trails of another, a fusion can occur. As both of these colonies lacked queens, some change or set of changes due to the absence of queens may be held responsible.

#### HABITAT AND NESTING

The area of the Southwestern Station in Cave Creek Canyon seems to be a very suitable habitat for certain *Neivamyrmex* species, from the fact that within ten weeks in this investigation more than 12 colonies of *Neiv. nigrescens* and 6 colonies of *opacithorax* were found operating within a zone of about 1,000 meters there. This spring-fed area presents a good range of nesting sites in dry to moist ground of varying composition, with a fairly good cover, and a large population of ground insects serving as booty. The typical pattern of operations in a nomadic colony is to raid the nests of ants and other insects from one site over a sector from 30 to 70 meters long, then to move on the same night into the subterranean diggings of one or more of the adjacent pillaged colonies or into some natural cavity. Colonies of *Formica* spp. and other ants are often thus dispossessed, the survivors usually huddling in the environs until the dorylines have moved on.

Although evidently the colonies of *Neiv. nigrescens* may extend their captured subterranean nesting sites to some extent through secondary excavation, typically they do not make their way along underground routes for more than a few meters. Although in nomadic raids the columns frequently run for considerable distances beneath ground cover, actual subterranean routes are infrequent and limited in extent. In statary raids, however, underground channels leading out from the nest commonly are utilized or developed to the extent that successive raids may originate on the surface at points several meters apart.

All nests involved in the present study were subterranean, often in the ground beneath stones as in the forcibly seized quarters of other ants, or with only the entrance holes exposed. The statary nest of Rock colony, excavated in detail on Sept. 5, occupied the central galleries and chambers of a fungus-ant's nest 1.2 m. broad and 1 m. deep, from which survivors had fled into peripheral zones with salvaged brood. Nomadic colonies of this species seem to cluster more numerous in central cavities, with their brood closer to the surface than in statary colonies, the nest patterns of which seem to be more extensive in breadth and depth.

### THE BROODS

In this investigation, the broods of both *Neiv. nigrescens* and *opacithorax* were found to occur in successive distinct generations. In the Meadow colony of the former species a major part of the brood estimated at more than 90 % was captured, and a randomized half of this collection numbered 17,354 individuals, which, doubled and including 2,336 specimens taken

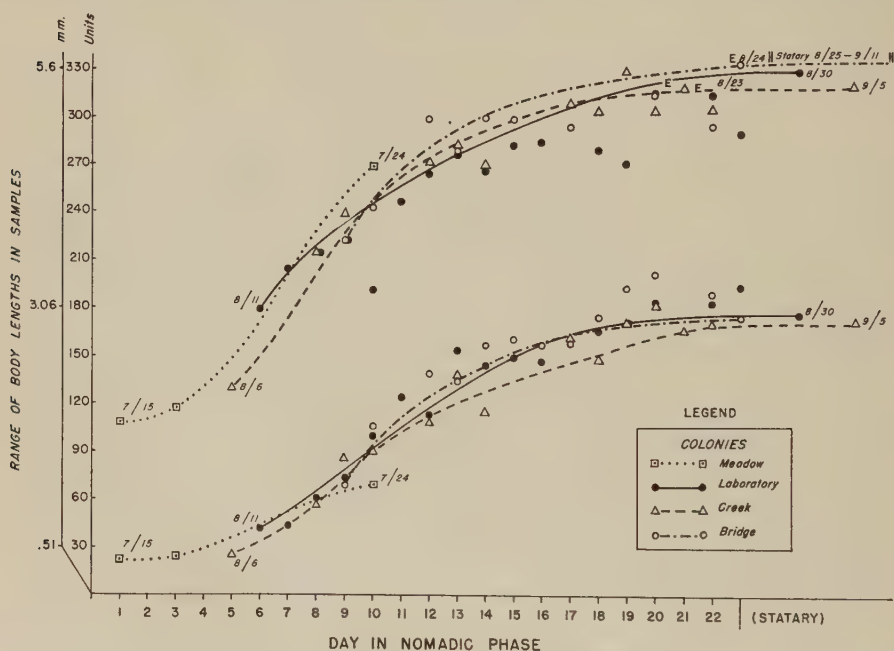


FIG. 6. — Maximal and minimal body lengths in brood samples taken from four colonies of *Neiv. nigrescens* at successive times from the early larval to the pupal stage of development. *E* on the curve of maxima marks the last emigration of the nomadic phase. The curves are synchronized on an empirical basis, and are smoothed in view of irregularities in sampling.

later from the colony remnant, indicates a total brood population of more than 37,000. From calculations based on repeated observations of the



same broods in successive colony emigrations, the strong impression was gained that under the conditions of this investigation this brood magnitude is usual for the species. These large broods, which are the rule, contain only potential workers. Evidently sexual broods appear infrequently and are much smaller, as in *Eciton*.

The concept of specific broods, each consisting entirely of individuals at nearly the same age, was invariably supported by the brood samples taken in this study. In the earliest large sample, that of the Meadow colony mentioned above, a randomized half numbering 17,354 individuals contained 95.5 % of embryos not exceeding 0.5 mm. in length and only 4.5 % of microlarvae up to 1.5 mm. in length. Figure 6 shows that successive samples taken from the larval broods of each of four colonies all present distinct upper and lower limits indicating a definite range of sizes increasing with further development.

The time interval between brood members first to eclose at pupal maturity and those last to eclose is estimated at about three days; probably an appreciably shorter time than the duration of egg-laying. The population curve of all-worker broods of this species is unimodal and skewed toward the smaller sizes. The largest members of the brood are the first to attain larval maturity, the first to attain the pupal condition, and the first to eclose as callows; the smallest members are the last in each case.

It is estimated that in the season of study, new broods were initiated regularly in the colonies at intervals of somewhat more than 35 days. The developmental period of a given brood from the egg to the mature pupal stage required a period of about 45 days, and an overlapping of broods therefore was the rule. The cases of the Meadow, Laboratory-A, Laboratory-B, Bridge, Thicket and Creek colonies of *Neiv. nigrescens* show that, in the regular season, a colony with a newly eclosed brood of worker callows also has a potential all-worker brood at the embryo-microlarval stage. If for the conditions of this study the case of the Bridge colony may be taken as representative, a procedure supported by comparison with the other cases in figure 6, the duration of brood development may be set at a value of nearly 50 days for these cases, on the assumption that egg-laying ended from 5 to 8 days before the nomadic phase began.

It is well known that the post-larval stages of brood development in *Neivamyrmex* species are naked. An interesting fact hangs thereon, namely, that when all-worker broods are present the last brood stage normally seen in colony emigrations before the colony enters the statary condition is early pupal, as in the case of the Bridge, Rock, and Creek colonies. Later stages preceding eclosion were taken in the Laboratory-B colony only by virtue of disturbance due to capture of the queen, in the Creek colony an abortive emigration, and in the Rock colony excavation of the statary bivouac. This interesting result will be considered in the Discussion.

In the two-day studies of the Rustlers' Road and Skunk Hollow colonies,

sexual-form larval broods were found as well as callow all-worker broods evidently only recently eclosed. Larval samples of about 25 specimens ranged from 6.5 to 8.7 mm. in body length in the former and from 6.4 to 7.8 mm. in the latter. From inspections of the emigrations, it was judged that neither of these broods numbered more than one or two thousand individuals at the most.

In the case of *Neiv. opacithorax*, two colonies were found with larval broods under transport in colony emigrations. The brood of Spring colony was estimated in the few tens of thousands and was clearly a potential all-worker brood, a large sample ranging 0.85-2.97 mm. in body length. The brood of Lodge colony seemed far less numerous and evidently included only sexual-form larvae, ranging 2.1-3.2 mm. in body length.

Notwithstanding the nightly practice of overturning rocks and other potential bivouac cover at every opportunity, no sexual brood of any species was found except for the two larval broods noted above and the winged males of seven *Neivamyrmex* species taken at the lights.

### THE EMIGRATIONS

In this investigation more than sixty emigrations of colonies of *Neiv. nigrescens* were observed. All of these colony movements occurred at night, and all as sequelae of raids. A case representing the relationship is sketched in figure 5. Typically, raiding activities went on for 2-3 hours or more before the emigration began with the emergence of a column moving outward from the bivouac including carriers of booty, brood from microlarval to semipupal stages, or with a mature brood mainly seen as callows running in the column, a minority transported as inert pupae. Emigrations seldom started within two hours after dusk when raiding began but usually were under way before midnight, or roughly within six hours after raiding began. Except with important interruptions as from rain or (late in the season) low temperature, the exodus from the old bivouac usually continued until it was finished or until dawn. The entire movement probably required about 6 to 8 hours as a rule. If not completed before daybreak, emigrations were continued on the following night, usually with an early beginning. Such a resumed emigration often went on simultaneously with an emigration from the current advanced site to a new bivouac. Even under the most disruptive conditions, such as heavy rain, or low temperature after midnight late in the season, no queenright colony was found to require more than two nights to carry out a change of bivouac. Also, no queenright colony ever emigrated along the back-trail, although, as with the Creek colony on August 19, an older section of trail might be followed if the colony happened to cross it after a period of days.

The emigration of *Neiv. nigrescens* involves a column of from 1-2.2 cm. in width, usually with a minority of returning traffic at the borders of

the procession, especially near the old bivouac or near the new site. In the early nomadic days, callows usually crowd the column until all have passed, and the young brood carried in packets may be expected during the latter part of the callow procession. When the larval brood is more advanced, its transportation generally starts within about one hour after a consistent exodus has begun. The queen, who runs the entire distance, always with a retinue of excited workers, usually makes her journey at some time after the emigration is roughly one-third completed.

The emigration always occurs over a principal trail developed from the bivouac in raiding (see figure 5). Often as the foray advances, the exodus moves up behind the forefront of raiding by stages, with the brood deposited in successive booty caches. Even when the exodus is fairly steady, the foray ahead of it presents a variety of traffic hindrances to the outgoing movement. Delays often occur at successive principal trail junctions where booty caches may afford opportunities for feeding by callows or by larvae. The emigration then is likely to forge ahead on the branch line presenting the lower pressure of returning traffic. For these reasons, establishing a new bivouac is often a variable and lengthy process.

While the nights remained temperate, emigrations were normally stopped only by their completion, by heavy and continued rain, or by the coming of daylight. However, in late August and early September in the area of study, nocturnal temperatures had fallen steadily to a point at which, by 2:00 a.m. in the more exposed places, the temperature was below 10° C. at the ground surface and only about 6-8°C. at 6 cm. above the ground. On such nights, at increasingly early times, raiding would slow down and presently stop, as would emigration. Emigrations requiring a second night for completion then were seen with greater frequency, particularly with colonies (e.g., Bridge) operating in more exposed areas. At times an emigration was completed on the second night without any further advance (e.g., Creek, August 23); at times the remainder of the colony would move up while an advance to a new site was under way (e.g., Bridge, August 18).

The distance of an emigration varied considerably. The shortest emigration observed in this study was a move of only 2.5 m. by the Laboratory-B colony on Aug. 15, the longest was one of 76 m. by the Bridge colony on August 23. The distances covered in successive emigrations by the Creek colony during the main part of a nomadic phase are listed in Table I. The emigrations of this colony, which may be taken as representative of the species under these conditions, ranged between 6 and 64 meters, with an average near 40 meters.

The new bivouac site reached in the emigration usually lay at a trail division somewhat short of the limits of raiding, but sometimes it was considerably short of that point, as in the case of the Creek colony on August 20. Occurrences in the emigration affecting the distance of the advance depend to a considerable extent upon the pattern of raiding. A frequent cause of shortened emigration is a heavy and continued return of



TABLE I.—DISTANCE COVERED IN SUCCESSIVE EMIGRATIONS OF CREEK COLONY,  
*Neiv. nigrescens*.

NOMADIC DAY (estimated).	DATE.	DISTANCE OF EMIGRATION.	NO EMIGRATION.
—	—	—	—
N-5	August 6	65 meters	
6	7	63 —	
7	8	...	X
8	9	46 —	
9	10	31 —	
10	11	47 —	
11	12	...	X
12	13	50 —	
13	14	6 —	
14	15	41 —	
15	16	...	X*
16	17	...	X*
17	18	36 —	
18	19	41 —	
19	20	18 —	
20	21	...	X*
21	22	40 —	**

\* Local shifting of brood.

\*\* Emigration completed over the same route.

booty-laden columns to a trail-junction cache at which the exodus has been halted. If such a place does not adequately accommodate the colony as its new bivouac, a further shift into the forward zone may occur once the pressure of return traffic is sufficiently reduced. Emigrations by stages, after this fashion, were often observed in this investigation.

### THE FUNCTIONAL CYCLE

The hypothesis of a distinct statary condition (23) in *Neiv. nigrescens* is supported by the results summarized in section A of Table II. These results indicate the existence of a phase of reduced colony activity and low excitement in which emigrations do not occur, coincident with the time when the brood is passing from the early pupal to the mature pupal condition. Among the colonies listed in Section A of Table II, Bridge represents the full course of this phase, Creek and Rock the beginning and principal part, and Stone and Thicket the terminal part.

The hypothesis of a distinct nomadic condition in *Neiv. nigrescens* is supported by the results summarized in section B of Table II. These results reveal the existence of a phase of vigorous colony activity and heightened excitement in which emigrations occur regularly, beginning with the eclosion of a mature pupal brood and normally ending at the time when the next generation reaches the early pupal condition. The



TABLE II.—NOMADIC AND STATARY FUNCTIONAL CONDITIONS AS INDICATED BY DISTINCTIVE CONDITIONS IN BROOD, EMIGRATIONS AND RAIDING \*.

A. <i>Neiv. nigrescens</i> , statary condition.			
COLONY.	BROOD CONDITION.	RAIDS.	EMIGRATIONS.
Creek	p to PP	14, all weak, in 17 days	1 in 17 days
Thicket	P to PP	3 weak in 3 days	0 in 3 days
Bridge	p to PP	15, all weak, in 17 days	0 in 17 days
Rock	p to P	6, all weak, in 9 days	0 in 9 days
Stone	P to PP	3, all weak, in 3 days	0 in 3 days
TOTALS.		43 in 49 days	1 in 49 days
B. <i>Neiv. nigrescens</i> , nomadic condition.			
Creek	Call., ml to p	15 strong, 3 med. in 18 days	13 in 18 days
Thicket	Call., ml	1 strong in 1 day	1 in 1 day
Bridge	Call. + L to p	15 strong, 1 med. in 16 days	12 in 16 days
Bridge	Call.	1 strong in 1 day	1 in 1 day
Pugsley	Call., ml	1 strong in 1 day	2 in 4 days (days 1,4)
Rock	p	2 strong in 2 days	1 in 2 days
Stone	Call.	4 strong in 4 days	2 in 4 days (days 1,4)
Lab. (A)	Call., ml	4 strong in 4 days	2 in 4 days (days 1,4)
Lab. (B)	Call., ml to L	13 strong, 2 med. in 15 days	13 in 15 days (none: days 2,3)
Skunk Hollow	Call. ♀♀, ♂ L	2 strong in 2 days	2 in 2 days
Rustlers Road	Call. ♀♀, ♂ L	2 strong in 2 days	2 in 2 days
TOTALS.		69 in 69 days	51 in 69 days
C. <i>Neiv. opacithorax</i> , nomadic condition.			
Lodge	Call. ♀♀, ♂ L	not obs.	2 in 2 days
Spring	♀ L	1 strong in 1 day	1 in 1 day
TOTALS.		1 in 1 day	3 in 3 days

\* Symbols: ml, embryos and microlarvæ; L, larvae; p, prepupæ; P, pupæ; PP, eclosion of mature pupæ; Call., callows. ---Broods are all-worker broods unless otherwise indicated.

Thicket, Laboratory-A and Pugsley records represent the initiation of this phase, Laboratory-B the initiation and principal part of the phase, Creek and Laboratory-B the principal part from just after the initiation to the completion, and Rock the completion. The Stone and Bridge records are considered representative of the initiation of this phase under exceptional seasonal conditions in which no young brood is present whose larval development would support a continuation of nomadism and whose attainment of the early pupal condition might be related to the processes normally terminating the phase (see figure 6).

In Sections *A* and *B* of Table II, the Creek, Bridge and Rock records represent the transition from the nomadic to the statary condition, with the first two showing that a nomadic sequence may precede. The Thicket, Bridge, Stone and Laboratory-B colonies represent the transition from the statary to the nomadic condition, with Laboratory-B demonstrating that a nomadic sequence may follow.

The records of the Bridge and Creek colonies each represent a nearly complete nomad-statory cycle. It may be inferred from the reliable indication of brood condition (fig. 6) that each of these colonies when found was already a few days advanced in the nomadic phase. It is apparent that each of these two colonies passed through virtually one complete cycle while under study.

Section *A* of Table II shows that in 6 of 49 nights in which six colonies with pupating broods were observed, no raiding occurred, and that raiding was rated as relatively weak in the others. This is a definite indication of a low level of colony activity, as is the fact that an emigration occurred in only one of the 49 cases. The one case occurred in the Creek colony after 12 nights with weak raiding and no emigrations, and was followed by 8 nights in a similar condition at the new site. Such an emigration is to be considered exceptional, particularly as a raid had started slowly and variably earlier in the evening, as do statary raids normally \*

These results contrast sharply with those in Section *B* of Table II, in which it is seen that raiding was rated as strong or at least medium in 69 of the nights with colonies having callow or larval to early pupal broods, and that emigrations occurred in 51 of the 69 cases. Various conditions relevant to certain of the failures to emigrate at such times may be mentioned. First of all, in four of these cases, an emigration occurred at the eclosion of a mature pupal brood but no further emigrations took place until the third night thereafter. It is possible that brood condition, alike in all four cases, had much to do with the interesting similarity in behavior, and we shall return to this point. The 10 remaining failures to emigrate under these conditions occurred sporadically and without indications of a reduced level of excitement in the colonies. For instance, in the Bridge colony, three successive nights without movement came at

\* Earlier in the evening, forays into a sector near the bivouac evidently had aroused extensive combat with two large colonies of *Pheidole* spp. nesting on that side. These ants may have spread into the doryline bivouac along subterranean channels, arousing an abortive emigration.

a time when raids were vigorous and highly productive, but involved many short and complexly branching trails. Comparable conditions existed in the Creek colony in two of the instances of failure to emigrate in the nomadic series. In these last cases, as also in the failure of specific emigration in the Bridge colony on August 22, much shifting of brood occurred along covered channels close to the bivouac. These cases will be considered in the Discussion.

The last two cases in Section *B* of Table II represent the coincidence of a condition of high arousal and of emigration in the colony, with the presence of a sexual brood in the larval stage. Unfortunately these colonies were on record only briefly, as were two cases of emigration in *Neiv. opacithorax* presented in section *C* of Table II, both colonies highly active with larval broods containing potential sexual forms in one and workers in the other.

Altogether, the results presented in Table II may be taken to indicate a close relationship in *Neiv. nigrescens* between condition of the brood and functional pattern of the colony. The prevalence of this correspondence of conditions through definite sequences of days in certain colonies representing successively the two different phases, and the reversal of each phase into the other under appropriate conditions of brood metamorphosis, are strongly indicated.

It is very interesting to note that the termination of a nomadic phase occurs not at larval maturation, as in *Eciton*, but only later when most of the brood has entered the early pupal condition. This important difference will be considered in the Discussion.

From the present results, the duration of the activity phases may be set very roughly, and only for the conditions of this investigation, at about 21-22 days for the nomadic phase and about 18 days for the statary phase. The correlation of brood curves in figure 6 indicates that in both the Bridge and Creek colonies nomadic function had begun a few days before these colonies were discovered in August. Although the curves in this figure lack common origin points and are synchronized on an empirical basis, the errors probably do not exceed one or two days. Only one completed statary phase was obtained,—that of the Bridge colony,—however, other results indicate the reliability of this case. For both phases, therefore, the above estimates are offered as good approximations of the respective time values for colonies operating in the locality of study under the prevalent seasonal conditions.

## DISCUSSION

From results for *Neivamyrmex* colonies under the conditions of this investigation, a reversible functional cycle prevails in the active season, describable as a nomad-statary cycle and theoretically equivalent to that found in *Eciton*. As in *Eciton*, cyclic function is continuous under appro-

prate seasonal conditions. However, in *Neivamyrmex* under Nearctic conditions, it is probable that the sequence of colony functional cycles is interrupted completely between autumn and spring.

From our present results, cyclic behavior in *Neivamyrmex* has its basis in reproductive functions, much as in *Eciton*. These two doryline genera seem equivalent in the effect of the two principal brood-excitatory factors promoting phasic changes in function: 1) a callow-excitatory factor initiating nomadism, and 2) a larval-excitatory factor continuing the phase. These major similarities prevail in function despite the fact that the *Eciton* species studied are terrestrial in nesting and regularly diurnal in raiding, the *Neivamyrmex* species hypogaic in their nesting and mainly nocturnal in surface activity. The hypothesis that homologous factors underlie the functional cycles of *Eciton* and *Neivamyrmex* seems to find support in these findings.

Two secondary characteristics distinguish the functional cycle of the investigated *Neivamyrmex* species from comparable aspects of *Eciton* function. The first is that, after an initial vigorous emigration on the eclosion of a mature pupal brood, emigration evidently goes into abeyance until about the fourth night. The resemblance of this occurrence to the early drop in nomadic function in *Eciton*, after a vigorous beginning (27, 28) seems unmistakable, and both phenomena may involve comparable processes associated with the overlapping of the mature pupal and young broods. The interesting difference is that although colony function in *Eciton* is somewhat reduced at a corresponding time, emigration does not stop, normally. The hypothesis may be advanced that in *Neiv. nigrescens* two factors are involved, the first postulated as a change in the responses of workers to the callow brood just after the initial highly excitatory eclosion episode, such that the colony although still very excited holds the same underground site without emigrating. The second factor postulated is a slower rise of the larval excitatory effect than in *Eciton*, related to a more retarded condition of the young brood. Results in the present study indicate that on the second and third nomadic days the bulk of the young brood is still in the embryonic and earliest microlarval stages. Tentatively, the break that appears characteristic of the early part of the nomadic phase in these *Neivamyrmex* is thus attributed to a temporary change in the worker-brood relationship, involving an inhibition of emigration by the specific post-eclosion influences of a callow brood together with a low stimulative effect from the young brood.

The second difference from *Eciton* is a striking one, related to properties centering around the absence of cocoon-spinning in the mature larval brood of *Neivamyrmex*. In this investigation, nomadic function continued in colonies of *Neiv. nigrescens* past the stage of maturity and straightening in the larval brood, and the statary condition did not ensue in the colonies until the naked brood entered the early pupal stage. This result is confusing at first, as the mature larvae soon lose the property of motility



and the *tactual* aspect of their stimulative effect on the worker population is inevitably reduced and greatly changed. For *Eciton*, I have held that the *tactual* stimulative effect of an active larval brood is a major factor promoting nomadism after the early part of the phase. However, in addition to the *tactual* factor in such trophallactic relations, a chemical factor must also be postulated (23, 27), which in *Eciton* falls greatly in strength at larval maturity. From the fact that in *Neiv. nigrescens* nomadism continues past the stage of larval maturation in the brood, an important difference would seem to exist between these dorylines and *Eciton* in respect to the brood-adult relationship prevalent at this time.

It seems that in *Neiv. nigrescens* the brood-stimulative effect somehow is held at a high level past larval maturation, despite a drastic reduction of the *tactual* factor. Laboratory tests of worker responses in this species to the inert brood stages between larval maturity and entrance into the pupal stage support the hypothesis that the stimulative factor critical for the maintenance of high worker excitement and nomadic colony function is chemoceptive, and presumably both gustatory and olfactory. The results suggest that the chemical effects involved are peculiar to this stage. The hypothesis is advanced that, during post-larval metamorphosis, products of stage-specific secretory and other metabolic functions are effective for which the organic basis is greatly limited or even absent in *Eciton*.

The reproductive properties of the relatively diminutive queen of *Neiv. nigrescens* are prodigious although not equal to those known for *Eciton* species. In the functional season this queen is capable of producing distinct broods at regular intervals, each new generation evidently initiated before the time-limited delivery of the preceding one as eggs has occurred, much as indicated for the *Eciton* queen by Hagan's (16) findings. For a reproductive individual of such limited body size to produce potential all-worker broods of around 40,000 individuals at intervals of no more than 40 days (as under the conditions of this investigation) is certainly impressive, but in keeping with the known properties of the doryline adaptive pattern (23, 27).

The conclusion held for *Eciton* (25, 27) that the timing of the queen's reproductive rhythm is not mainly dependent upon endogenous processes, but rather upon a complex set of interrelationships between the queen and the colony situation, seems also valid for *Neiv. nigrescens* as represented in this investigation. In this doryline also, the regularity of brood generations produced by the queen seems attributable to an interplay of exogenous and endogenous factors affecting the queen's reproductive functions. But it is possible that under Nearctic conditions the temporal control of reproductive processes in the doryline queen and colony may differ according to the state of brood development and related feed-back processes keyed to prevalent seasonal conditions in temperature and food supply particularly. This possibility remains to be tested.

Present evidence indicates a termination of reproductive function in the autumn. But the cessation of seasonal reproductive processes in the queen may not occur quite as abruptly as certain cases in this study would indicate. At a time dependent upon locality and altitude, a transitional interval may ensue before full dormancy sets in, when reduced broods are produced by the queen but are lost perhaps through worker cannibalism. Such a condition was possible in the Thicket, Bridge and also the Stone colonies, but seems very unlikely in the cases of the Rock and Creek colonies. The last cases instead support the concept of a definite threshold of exogenous stimulative and trophic conditions below which the queens become non-functional.

The latter interpretation seems to account best for the general results. In Arizona, at an elevation of one mile, the duration of nightly colony raiding seemed to be steadily reduced after late August, particularly through falling temperature which stopped surface activities at increasingly early times. Then the food intake of the colony might clearly undergo a rapid decrease as not only the nightly foraging time became greatly curtailed but also raiding activities became increasingly sluggish. For the colonies involved in the longitudinal surveys of this study, it is probable that functional phases begun under the trophallactic effect of broods maturing after late August would have ended before one month, and would have been succeeded by a non-cyclic, dormant, over-wintering condition. It is probable that this condition would have arisen as a normal seasonal change, even had these colonies retained their queens.

As it was in the autumn of 1956, with the six queenless colonies left in the Station area of Cave Creek Canyon, the prospects for a later resumption of cyclic function must have depended not only upon surviving the winter but also upon the chances of fusion with queenright colonies of their species upon reactivation in the spring.

## SUMMARY AND CONCLUSIONS

An investigation was made of behavior and biological function in several colonies of the Nearctic doryline species *Neivamyrmex nigrescens* at an altitude of 1,660 m. in Arizona. In that locality this species is subterranean in its nesting and is nocturnal in its raiding and emigrating, except for surface forays on overcast days. Under appropriate stimulative conditions in the colony, a vigorous raid provides a basis for an emigration during the same night.

These dorylines resemble *Eciton* species of the tropics in having a distinct nomadostatory cycle. This cycle in colony function is dependent upon critical stimulative effects from the successive immense, distinctive all-worker broods, and thus is repetitive in each colony during the active season.

In these army ants each nomadic phase is set off, as in *Eciton*, by a massive stimulative effect introduced upon the eclosion of a mature pupal brood, and is then maintained by stimulative excitation from a new brood in the larval stage. In striking contrast to *Eciton*, the nomadic phase in this *Neivamyrmex* species does not end at larval maturity, but only later when the current brood reaches the early pupal stage. No cocoons are spun by mature worker larvae in this genus, and the high excitatory

effect evidently is continued through an intensive chemotactic excitation characteristic of the developmental period between larval maturity and attainment of the early pupal condition.

Onset of the statary phase is attributable to an abrupt fall in the potency of brood stimulative processes as the brood begins to enter the pupal stage.

In the locality of study, the functional season terminated during September, evidently at a time after the colony queen had ceased to produce mature eggs in large broods. This change may depend upon a seasonally conditioned reduction of stimulative and trophic conditions in the colony below a specific threshold essential for normal reproductive function in the queen.

It is concluded that the factors underlying a regular cyclic function in colonies of *Neivamyrmex nigrescens* during the active season are basically equivalent or even homologous to those operative in *Eciton* species, and that the differences may be considered secondary.

## RÉSUMÉ ET CONCLUSIONS

Une enquête a été effectuée sur le comportement et sur la fonction biologique chez plusieurs colonies de l'espèce néarctique de fourmi doryline *Neivamyrmex nigrescens*, à l'altitude de 1 660 m dans l'État américain de l'Arizona. En ces lieux, l'espèce est souterraine quant à ses nids et est nocturne quant à ses raids et déménagements, sauf en cas de razzia par temps couvert. Dans des conditions appropriées d'effet stimulant dans la colonie, un raid très violent sert de base à une émigration au cours de la même nuit.

Ces dorylines ressemblent aux espèces *Eciton* des tropiques, en ce sens qu'elles sont soumises à un cycle caractéristique nomadisme-sédentarité. Ce cycle fonctionnel de la colonie dépend des effets stimulants critiques provenant des immenses couvains distinctifs composés uniquement d'ouvriers, et il se renouvelle donc dans chaque colonie pendant la saison d'activité.

Chez ces fourmis guerrières, chaque phase de nomadisme est déclenchée, comme chez *Eciton*, par un effet stimulant massif dont l'origine se trouve dans l'éclosion d'un couvain nymphal parvenu à maturité, et elle se maintient ensuite par l'excitation stimulante due à un nouveau couvain à l'état larvaire. Par un contraste saisissant avec ce qui se passe chez *Eciton*, la phase nomadique chez cette espèce de *Neivamyrmex* ne prend pas fin lors de la maturité des larves, mais seulement plus tard lorsque le couvain en cours de développement est arrivé au stade nymphal. Chez ce genre, les larves mûres d'ouvriers ne tissent pas de cocons, et la cause excitatrice si vive se poursuit évidemment sous l'influence d'une intense excitation chémo-tactile, qui est caractéristique de la période de développement située entre la maturité larvaire et l'arrivée de la première forme nymphale.

Le déclenchement de la phase de sédentarité doit être attribué à une brusque diminution de puissance des facteurs stimulants chez le couvain, tandis que celui-ci commence à entrer dans le stade nymphal.

A l'emplacement des études effectuées, la saison d'activité fonctionnelle



s'est terminée dans le courant de septembre, à une époque qui se situe évidemment après que la reine de la colonie eut cessé de produire des œufs mûrs en importants couvains. Ce changement dépend peut-être d'une réduction, en temps opportun, de facteurs stimulants et trophiques dans la colonie, en deçà d'un seuil spécifique qui est essentiel à l'exercice normal de la fonction reproductrice de la reine.

En conclusion, les facteurs qui sont à la base d'une fonction cyclique régulière chez les colonies de *Neivamyrmex nigrescens*, pendant la saison d'activité, sont sensiblement équivalents ou même homologues de ceux qui entrent en opération chez les espèces d'*Eciton*, et les différences peuvent être considérées comme secondaires.

### Zusammenfassung.

Verhalten und biologische Function in mehreren Kolonien der nearktischen Ameisen-Art *Neivamyrmex nigrescens* (Unterfamilie Dorylinae) auf 1 660 m. Seehöhe in Arizona wurden untersucht. Dort nistet diese Art unterirdisch und unternimmt ihre Raubzüge und Auswanderungen zur Nachtzeit, ausgenommen Oberflächen-Razzias an bewölkten Tagen. Unter geeigneten Stimulationseffekten innerhalb der Kolonie löst ein kräftiger Raubzug fast unfehlbar Auswanderung noch in derselben Nacht aus.

Diese Dorylinen ähneln tropischen *Eciton*-Arten in ihrem deutlich nomadisch-statischem Zyklus. Dieser Zyklus in der Function der Kolonie hängt von kritischen Stimulationseffekten aufeinanderfolgender, sehr großer, deutlich nur aus Arbeitern bestehender Bruten ab, und wiederholt sich so in jeder Kolonie während der Aktivitätsperiode.

Wie in *Eciton* so wird auch in diesen Dorylinae jede nomadische Phase durch den massiven Stimulationseffekt des vollen Heranreifens einer Puppenbrut eingeleitet und dann durch stimulative Erregung durch eine neue Brut im Larvenstadium wach gehalten. Im auffallenden Gegensatz zu *Eciton* endet jedoch in dieser *Neivamyrmex*-Art die nomadische Phase nicht mit der Larvenreife, sondern erst bis die jeweilige Brut das pupale Stadium erreicht. In dieser Gattung spinnen die reifen Arbeiterlarven keine Cocons; der starke Erregungseffekt wird offenbar durch intensive chemotaktische Erregung, eine eigenartige Begleiterscheinung der Metamorphose, aufrechterhalten.

An der untersuchten Örtlichkeit endet die Functionsperiode im September, offenbar sobald die Königin der Kolonie aufgehört hat, neue Bruten hervorzubringen. Möglicher Weise hängt diese Veränderung von einer jahreszeitlich bedingten Verminderung der stimulativen und trophischen Bedingungen unter eine kritische Schwelle ab.

Hieraus wird gefolgert, daß die der regelmässigen zyklischen Function in Kolonien von *Neivamyrmex nigrescens* während der Aktivitätsperiode zugrunde liegenden Faktoren im wesentlichen den in der Gattung *Eciton* wirksamen gleichwertig oder selbst homolog sind und daß die Unterschiede als sekundär werden können.

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# NOUVELLES DE L'UNION

## TRAVAUX PUBLIÉS PAR DES MEMBRES DE L'UNION

BORGMEIER (Thomas). — **Die Wanderameisen der Neotropischen Region**, O. F. M. Studia Entomologica, Nr. 3 (Editora Vozes Ltda., Caixa Postal 23, Petrópolis, Rio de Janeiro, Brazil), 720 p., 87 pls., paper. Price \$ 15.00 U. S.

Diese Monographie ist in ihrer Gediegenheit eine vorbildliche Leistung des weltbekannten Myrmekologen; sie wurde in Fachkreisen längst mit Spannung erwartet. Wie kein anderer war Borgmeier berufen, in dem System der Ecitoninen Ordnung zu schaffen und so nach langjährigen intensiven Studien den Grund zu legen zur weiteren Vertiefung unserer Kenntnisse über die Morphologie und Biologie der 140 bekannten Arten. Zugleich schuf der Autor hiermit eine zuverlässige Grundlage für die Erforschung der zahlreichen ecitophilen Insekten, die von Wasmann begonnen und von Reichensperger erfolgreich fortgesetzt wurde und auch die vielen, damit in Verbindung stehenden ökologischen und tier-geographischen Probleme fußen auf dieser Monographie.

Allgemein richtungsgebend sind zunächst die Darlegungen über die Grundfragen der Systematik: ungewöhnlich reichhaltige Beobachtungen und deren ausgereifte, vielseitige gedankliche Durchdringung, dazu objektive Beschränkung auf das wissenschaftliche Feld der Tatsachen geben hier der Systematik als Wissenschaft neue erfreuliche Impulse. „Die beobachteten phaenotypischen Merkmale und Ähnlichkeitsbeziehungen wurden nicht etwa gezählt, sondern gewertet.“ Und dazu ist eben der Blick des erfahrenen Forschers notwendig, der weder mit „Mengenlehre“ noch mit „mathematischer Logik“ aufgewogen werden kann.

Zu dem Verhältnis zwischen Systematik und Phylogenie wird bemerkt: „Die Systematik ist unabhängig vom Deszendenzgedanken“, „die Phylogenetik basiert zum größten Teil auf den Tatsachen der Systematik“. Auch mit den Beziehungen der Systematik zur Genetik setzt sich der Verf. auseinander; es wird Stellung genommen gegen das Bestreben gewisser Genetiker, „den Artbegriff zu pulverisieren“. Borgmeier kommt zu dem Schluß, daß die Art eine Fundamenteinheit des Systems ist. „Die Art ist ein Wesens- und Ganzheitsbegriff, der auf objektiven Gegebenheiten beruht“ und „nicht erst vom Menschen in die Natur hineingetragen wird. Der biologische Artbegriff ist keine Erfindung der „Neuen Systematik“, sondern von alters her vertreten worden. Kopulationsbereitschaft bzw. Kopulationsabneigung werden als Kriterium für die Art nicht anerkannt, desgleichen geographische Faktoren in der Artssystematik abgelehnt. Ein weiteres Kapitel befaßt sich mit der Subspezies oder Rasse als Unterkategorie der Art. Wie sonst im Tierreich gibt es bei den Ameisen neben monomorphen Arten pleomorphe. „Alle Rassenbildung vollzieht sich streng innerhalb der Artgrenzen.“ „Arten sind wesentlich verschieden, Rassen sind wesentlich gleich, weil sie in den Grundmerkmalen übereinstimmen und zu derselben Fortpflanzungsgemeinschaft gehören.“ Alle Rassen zeigen das „Gesicht“ der Art, von der sie sich abgespaltet hat. Unter „Artgesicht“ verstehe ich den Komplex aller spezifischen Merkmale, welche allen Rassen derselben Art gemeinsam sind. „Alle Arten, mögen sie auch auf den ersten Blick noch so ähnlich sein, sind scharf getrennt, sobald man nicht von einem Individuum ausgeht, sondern den gesamten Merk-

malskomplex in Betracht zieht.“ „... die Tatsache, daß die Artmerkmale bei jeder Rassenbildung erhalten bleiben, spricht recht eindeutig für die Bildung von Rassen aus Arten, nicht aber von Arten aus Rassen.“

Die in der älteren Myrmekologie seit 1890 von Emery eingeführte infrasubspezifische „Varietät“ wird von Borgmeier als taxonomische Kategorie abgelehnt.

Der spezielle Teil wird eingeleitet von Erörterungen über die Grenzen der Subfam. Dorylinae und bringt eine Tribus-Einteilung. Das Hauptgewicht zur Unterscheidung wird auf die Genitalien gelegt. Folgende Haupteinteilung wird getroffen: I. Cheliomyrmecini und Ecitonini; II. Dorylini, Aenictini und Aenictogitonini.

Zu zahlreichen eigenen Neubeschreibungen kommen hinzu langjährige Typenstudien; sehr sorgfältige Zeichnungen der Kopfformen, besonders der Genitalien, Photogramme von Flügeln ergänzen in anschaulicher Weise die Beschreibungen.

Der taxonomische Scharfblick und die ausgesprochene Begabung einer präzisen Beschreibung und Darstellungsweise Borgmeiers gestalten die Monographie zu einem vorbildlichen Standardwerk der Systematik. Als besonderes Verdienst sei auch das sorgfältige Eingehen auf Synonyme (60 Namen fallen darunter) erwähnt, die bisher in der Systematik mitgeschleppt wurden.

Die Bearbeitung der einzelnen Arten umfaßt jeweils: Synonyme, Holotype bzw. Typen und Cotypen, Beschreibung der Kasten, z. T. Originalbeschreibungen, geographische Verbreitung, untersuchtes Material, Variationen, Diskussion. Zahlreiche biologische Notizen ergänzen die systematische Bearbeitung, z. B. über Nester, Züge, Orientierung, Feinde von Geschlechtstieren, eingetragene Beute, mitgelaufene Gäste aus der Gruppe der Staphyliniden, Histeriden, Phoriden.

Eine systematische Uebersicht der Gattungen und Arten, ein sehr umfangreiches Literaturverzeichnis, Erläuterungen zu den 87 Tafeln, dazu ein alphabetisches Register der Personen-Namen, der Gattungen und höheren Kategorien, ferner der Arten, Unterarten und Varietäten (jeweils mit durch Druck hervorgerufenen Synonymen) und eine Inhaltsübersicht rundet dieses vortreffliche Werk ab, das weit über den Rahmen der Myrmekologen — vor allem wegen der grundsätzlichen Erörterungen über die Probleme der Art- und Rassenforschung — in allen biologisch ausgerichteten Bibliotheken verbreitet zu werden verdient. Noch nie wurde eine Teilgruppe der Formiciden so umfassend und gründlich bearbeitet.

GÖSSWALD (Würzburg).

## ANALYSES DE TRAVAUX

HÜSING (J. O.). — *Die Honigbiene (Apis mellifica L.). 2. neubearbeitete Auflage. 99 S., 46 Abb. Akad. Verl. Ges. Leipzig, 1942 (H. 31). Preis...*

Die Bienenarbeit umfaßt folgende Kapitel: Vorwort, zur Geschichte der Staatswerdung des Bienenvolkes, Rassen der Honigbiene, Drohnen, die Königin, die Arbeitsbiene, die Ammenbiene, die Wachsbienne, die Wehrbiene, die Trachtbiene, Brutordnung, Bienenwohnung und Bienenstand, Bienen und Blüten, Orientierungsfähigkeiten und Sprache der Bienen, Arbeiten am Bienenstand im Laufe des Bienenjahres, Krankheiten und Feinde der Bienen, Literaturhinweise.

Der Stoff ist übersichtlich, unter Einhaltung wissenschaftlicher Exaktheit auch für den Laien leicht verständlich und durch gute Abbildungen veranschaulicht dargestellt. Zur Verbreitung bei Biologen sowie bei Imkern ist es sehr gut geeignet und wird auch bei allen Naturforschern zur leichten Orientierung beste Dienste leisten.

GÖSSWALD (Würzburg).



SCHMIDT (H.). — *Die Termiten. Ihre Erkennungsmerkmale und wirtschaftliche Bedeutung. 309 Seiten, 120 Abb. Akad. Verl. Ges., Leipzig, 1955.*

Das Buch des bekannten Termitenforschers enthält Beiträge aus den reichen Erfahrungen H. Weidners über Körperbau, Systematik, Verbreitung der Termiten, ferner Termitennester und die Bekämpfung der pflanzenschädlichen Termiten. Weiter berichtet A. Herfs über die bestens eingerichtete Termitenstation der Farbenfabriken "Bayer" AG. in Leverkusen (Rheinland) in Verbindung mit Beiträgen über das Schwärmen und die Koloniegründung der Termiten. K. Gößwald hat das Kapitel: Die Gebälstermite (*Calotermes flavicollis* Fabr.) als Versuchstier bearbeitet, H. Schmidt den Abschnitt: Termitenangriff und Holz, unter besonderer Berücksichtigung des Bau und Werkholzes. IV. Sandermann stellt die chemischen Grundlagen der Holzschutzmittel gegen Termiten und ihre Anwendungsverfahren dar. W. Bavendamm kennzeichnet die natürliche Dauerhaftigkeit der Hölzer gegen Termitenfraß. Ein Sachregister ist beigelegt.

Der übersichtlich dargestellte reichhaltige Stoff des Termitenbuches dürfte weites Interesse finden, vor allem auch seitens der angewandten Forschung und der Termitenprüfstellen; zur Ergänzung rein zoologischer Fragen wird auf die von P. P. Grassé bearbeitete hervorragende Termitenmonographie in dem großen Standardwerk: *Traité de Zoologie*, Bd. 9, Paris, 1949, verwiesen.

GÖSSWALD (Würzburg).

## LISTE DES TRAVAUX DU LABORATOIRE DE PHYSIOLOGIE ACOUSTIQUE

de l'Institut National de la Recherche Agronomique, JOUY-EN-JOSAS (Seine-et-Oise),  
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